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AN INVESTIGATION OF CROSS-SHELF VARIABILITY IN SHELF CIRCULATION IN THE NORTHWEST GULF OF MEXICO[1]

Ned P. Smith

Harbor Branch Foundation, Inc., RR1, Box 1 6, Fort Pierce, Florida 33450, U.S.A.

ABSTRACT

Recording current meter data from two study sites, 6 and 34 km off the central Texas Gulf coast are compared for a 36-day period in the spring of 1977. Nearshore motion over the mid and inner continental shelf exhibits many of the characteristics which support the concept of a coastal boundary layer lying within approximately 10 km of the coast. Cross-shelf variations in longshore and cross-shelf current components, and in the coherence between longshore motion and the longshore component of the windstress suggest that several distinctions exist between current patterns in inner and mid shelf waters. Energy density values computed from cross-shelf current components are consistently greater over all but the shortest time scales at the outer station. Energy density values computed from inner shelf longshore component current data are greater over time scales in excess of approximately five days. Low-frequency longshore motion at the inner station is coherent with the longshore component of the windstress only at periodicities in excess of approximately five days. Longshore motion at the outer station is coherent with longshore windstress over time scales generally between one-half and five days.

INTRODUCTION

One of the dominant characteristics of the circulation of coastal waters is the spatial variation across the shelf of both the longshore and cross-shelf components of the current. Cross-shelf motion over the inner shelf is constrained by the adjacent coastline, and rotary tidal or inertial motions are damped and may be reduced to oscillations in the longshore component of the flow. The response of coastal waters to air-to-sea momentum fluxes is related directly to water depth in the absence of density stratification. This produces strong cross-shelf gradients in the longshore component of the current. The kinetic energy associated with nontidal motions may decrease with distance from the coast, as nearshore motion is accelerated to greater speeds and is more easily reversed by variations in the longshore component of the windstress.

Investigations of nearshore motion conducted over the past few years have documented consistencies in circulation patterns recorded along cross-shelf transects, and thus utilized these spatial variations to distinguish between the current

[1] Harbor Branch Foundation, Inc., Cont. No. 186.

regime characteristic of the inner shelf and that occurring in mid and outer shelf waters. Specifically, a Coastal Boundary Layer (CBL) has been described by Birchfield and Davidson (1967), Csanady (1972, 1977), and Blanton (1974, 1975a, 1975b). Within approximately the innermost 10 km of shelf waters, rotary tidal and inertial motions are suppressed, and the kinetic energy associated with low-frequency longshore motion becomes relatively dominant.

Verber (1966) first reported a clear distinction between rotary motion, recorded 20 km offshore in Lake Michigan, and what was termed "straightline flow," recorded only 5 km offshore. Blanton (1974) used current data from Lake Ontario to demonstrate an abrupt increase in low-frequency motion (periods in excess of three days) and an equally abrupt decrease in inertial period motion at a point nominally 8 km from the shore. This feature was especially pronounced under stratified conditions during the summer months.

Early studies of the CBL were restricted largely to the Great Lakes. In addition to the reports noted above, data obtained in Lake Ontario during the International Field Year on the Great Lakes, have been discussed by Csanady and Scott (1974), and nearshore variations in current patterns have been noted for Lake Superior by Smith (1972). Studies of continental shelf circulation have increased significantly over recent years, but station density is often too low to resolve adequately the characteristics of a zone lying within 10 km of the coast.

A series of shelf circulation studies has been conducted over the past several years in the northwestern Gulf of Mexico to document both general seasonal patterns and the vertical and horizontal gradients in waters over the inner and mid shelf (Smith 1975, 1978). Motion along the Texas coast can be characterized as having generally north-to-south flow between approximately November and April, and a relatively slow alternating flow, with a slight net transport to the north, during the summer months. Circulation along the Texas shelf is isolated from the permanent circulation systems of the Gulf and appears to be driven by the longshore component of the local windstress.

More recently, a second generation of field studies has been conducted to investigate vertical current structure (Smith 1979) and longshore coherence along the central and lower Texas coast (Smith 1980). The work reported in this paper represents the third component of these more highly focused studies, in which the cross-shelf variation in current patterns is considered. This study was not designed specifically to delineate the spatial limits of the CBL in shelf waters off the Texas Gulf coast, but the data are interpreted logically in terms of the general description of the CBL compiled from previous studies. The purpose of this paper is to make a quantitative comparison of the current patterns recorded at inner and middle shelf stations, both within and outside of the nominal limits of the CBL. Results should be useful for extending the CBL concept to oceanic settings.

THE OBSERVATIONS

The study period was a 48-day period, from 10 March through 26 April 1977. Within this time interval, both stations were in operation during the 36-day period from 22 March through 26 April. At this time of year the water column is well mixed, with little vertical variation in

temperature or salinity. Winds affecting shelf waters during the spring months are neither as persistently onshore as they become during the mid and late summer months, nor as variable as during the winter months, when cold fronts move across the Texas coast.

Recording current meters were located at two stations, 6 and 34 km off the central Texas Gulf coast (Fig. 1). Environmental Devices Corporation Type 105 current meters at the inner station were placed 2 and 10 m above the bottom in 15 m of water. At the outer station, current meters were positioned 5,12,19 and 26 m above the bottom on a taut-line mooring in 33 m of water. Isobaths closely parallel the coastline at both the inner and outer study site. The local cross-shelf gradient is approximately 0.93 m/km, and there are no prominent bathymetric features along this part of the continental shelf.

Current measurements were time-integrated over half-hourly or hourly sampling periods. The accuracy in speed and direction was $\pm$ 1.8 cm/sec and $\pm$ 7°, respectively, according to the manufacturer's specifications. Coastal wind data were obtained from an anemometer located 0.5

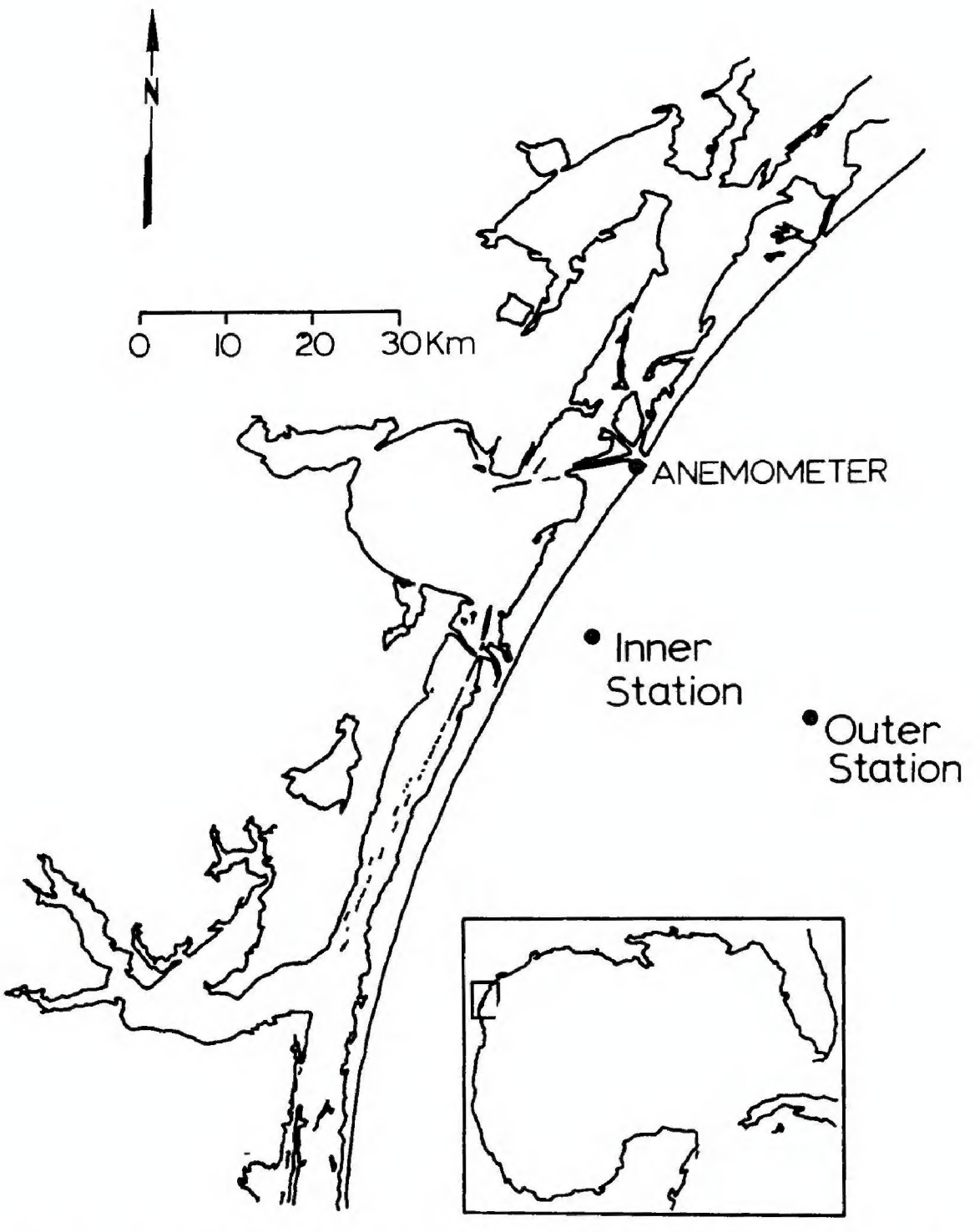

FIG. 1. Inner and mid shelf current meter mooring sites, and location of anemometer at Port Aransas, Texas. Insert shows the study area in the northwestern Gulf of Mexico.

km from the coast at Port Aransas, Texas, and 21 and 36 km from the inner and outer current meter stations, respectively. The sensor was mounted on a 33 m tower, the base of which was approximately 2 m above mean sea level. North-south and east-west component wind speeds were recorded in analog form, read at hourly intervals to the nearest mile per hour, and converted to longshore and cross-shelf windstress components, using the method suggested by Wu (1969) for moderate wind speeds. The precision of the computed windstress was approximately $\pm$ 0.04 to $\pm$ 0.17 dyne/cm^2 within the speed range characteristic of the study period.

RESULTS

The progressive vector diagrams (PVDs) provide an appropriate starting point for a description of the general characteristics of the circulation at the two study sites. At the inner station, 6 km from the coast, a composite of the PVDs constructed from current measurements made 2 and 10 m above the bottom is shown in Figure 2. At the lower level, the pattern can be characterized as quasi-steady in direction and deflected approximately 30° offshore of a true longshore heading. There is some meandering in the current, and during one period of approximately 4 days, the flow veers sharply clockwise and moves nearly directly onshore. During the 36 days that the inner station was in operation, 281 km of water moved past the current meter in a longshore direction, and 190 km of water moved past in an offshore direction. From this, a resultant current vector was obtained which had a speed of 10.8 cm/sec and a heading of 179°, or 34° to the left (offshore) of the local coastline (033°–213°).

At the upper level, 10 m above the bottom and nominally 5 m below the surface (tidal range is approximately 1 m), the PVD indicates a current with distinctly different characteristics. The flow at this level was tightly constrained by the coastline. Midway through the record, there was a significant reversal in the longshore component of the current for approximately 6 days. The current then continued to follow closely the local coastline and the 15 m isobath. From the endpoints of the PVD, a resultant current speed of 13.8 cm/sec was obtained; the resultant direction was 214°, or 1° to right (onshore) or a true longshore direction. This may not be physically meaningful, however, in view of the precision of the current meter. It is noteworthy that there was no clear indication of rotary oscillations at either level at this location, and that tidal and inertial period meanders in the longshore motion are minimal.

Current data from the outer station, obtained between 10 March and 26 April, are shown in Figure 3. At a level 5 m above the bottom, the PVD shows motion which closely parallels the 33 m isobath. There are two current reversals during the study period, and the flow during the last four days is nearly directly onshore. The resultant current speed was 6.8 cm/sec; the resultant direction was 217°. This heading was 4° to the right (onshore) of a longshore direction.

The PVDs from 12 and 19 m above the bottom are similar to pattern recorded 5 m above the bottom. Thus, it appears that vertical variations in speed and direction were slight during this time period through the lowest four-fifths of the water column. At a level 12 m above the bottom, the resultant speed was 11.1 cm/sec and the resultant heading was 210°. At 19 m above the bottom, the resultant speed

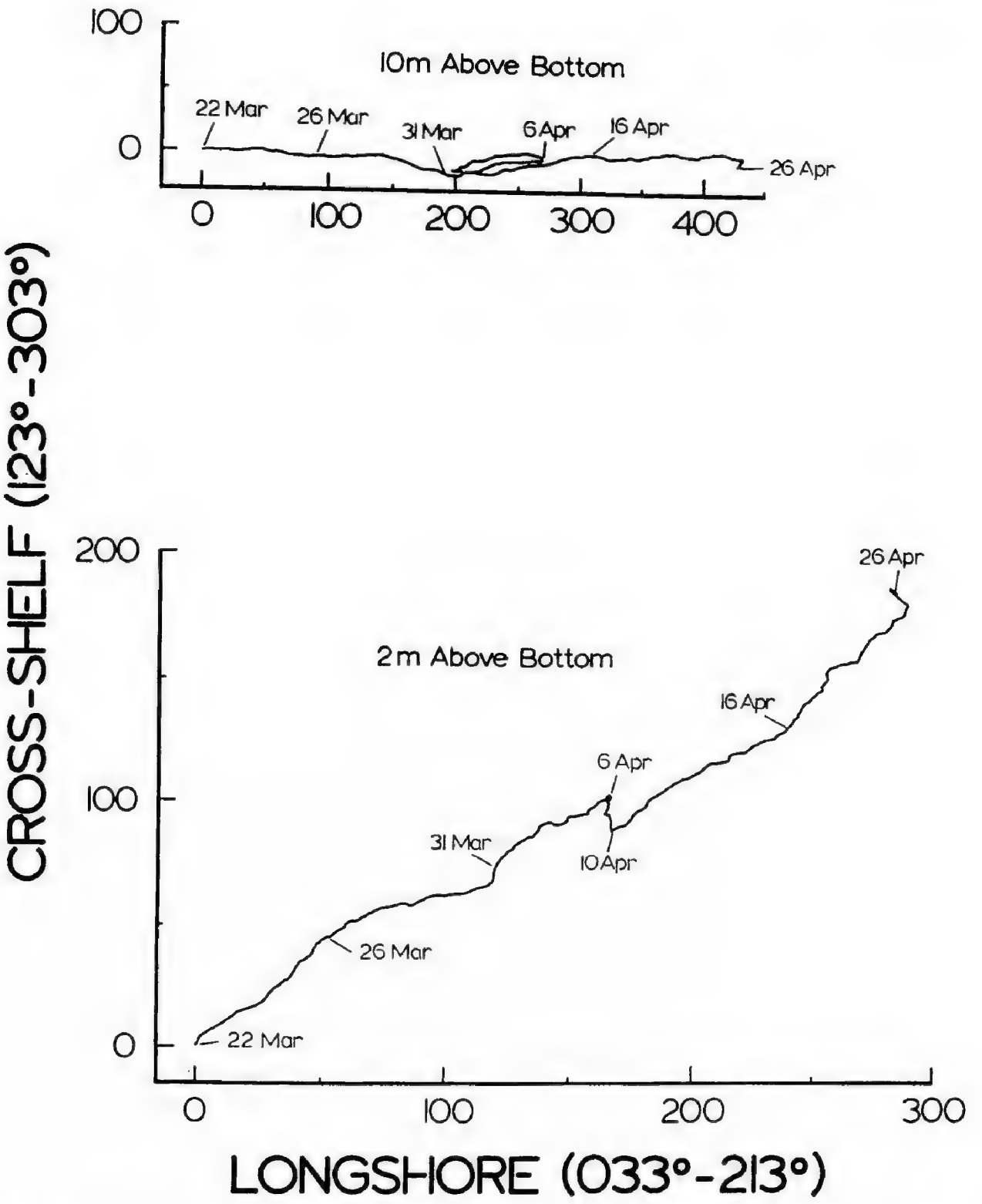

FIG. 2. Composite of progressive vector diagrams for currents measured 2 and 10 m above the bottom in 15 m of water at the inner station, 22 March through 26 April, 1977. See Figure 1 for station location.

was 13.3 cm/sec and the resultant direction was 207°. This suggests a slight counter-clockwise deflection with height above the bottom, but the difference in headings must be interpreted in light of the accuracy of the current meter, as noted above.

A distinctly different pattern is indicated by the time series from the top current meter. At this level, 26 m above the bottom and nominally 7 m below the surface, the PVD indicates a current with a distinctly offshore deflection—much like the pattern recorded 2 m above the bottom at the inner station (Fig. 2). The

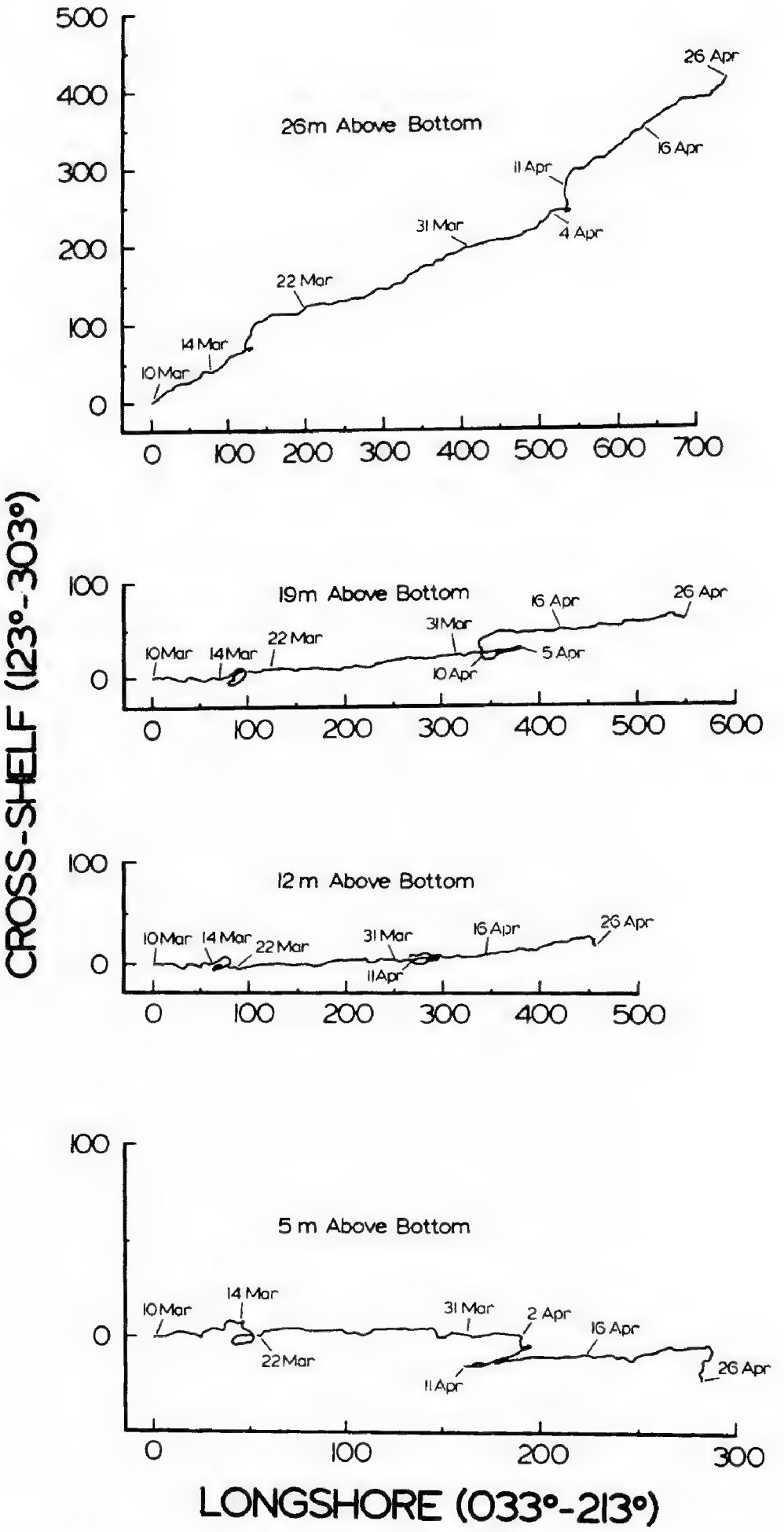

FIG. 3. Composite of progressive vector diagrams for currents measured 5, 12, 19 and 26 m above the bottom in 33 m of water at the outer station, 10 March through 26 April 1977. See Figure 1 for station location.

two time periods during which the current reversed at greater depths in the water column appear here as periods of little or no current. Over this 48-day time interval, the resultant current vector had a speed of 20.5 cm/sec and a resultant direction of 184°, or 29° to the left (offshore) of the local longshore direction. It is again noteworthy that rotary motions are not present in the time series from the outer station. A periodic meandering in the cross-shelf component of the flow is apparent at the uppermost level only.

The quantitative comparison of current data from these two sampling locations is provided by a spectral analysis involving the longshore and cross-shelf current components (Fee 1969), and the windstress affecting shelf waters at both sites. In this paper current data recorded at the uppermost level on each mooring are compared. Mid depth measurements were not available from the inner station, and it is not the intention to investigate cross-shelf variations in the benthic boundary layer.

Figure 4 shows the spectra of cross-shelf motion at the uppermost level at each station, and the resulting differences of the base-10 log of the energy density values. Positive values indicate greater energy density levels at the inner station. Several points are noteworthy. Energy density values in the long-period part of the spectra are distinctly higher for cross-shelf motion recorded at the outer station. This is especially true at the approximately diurnal tidal and inertial periodicities, where energy density values are nearly an order of magnitude higher at the outer station. At periodicities below approximately 4 hours, however, the two spectra are not distinctly separated, suggesting that these higher frequency motions are not constrained by the coastline at either location.

The spectra of longshore motion at the two study sites are shown in Figure 5. The distinction is somewhat less clear for the spectra as a whole. At the very longest periodicities, energy density levels are highest in the inshore record. The curves cross at a period of approximately 96 hours, however, and over a broad range of time scales surrounding and including tidal and inertial periods, higher energy levels are computed from currents recorded at the outer station. At a period of approximately 10 hours, the curves again cross, and energy density levels computed from the nearshore record are higher until the curves converge at the short-period end of the spectrum.

The coherence of both longshore and cross-shelf component motion recorded by the top current meters at these two stations is shown in Figure 6. Statistically significant values are found only for time scales in excess of approximately 5–6 days in the spectrum of longshore motion. At shorter periods, including the diurnal tidal and inertial periodicities, there is no significant relationship in longshore flow at these two locations. The cross-shelf component of the current is also coherent across inner and middle shelf waters over the longest time scales, though highest coherence-squared values are somewhat lower than those computed from the longshore components. Coherence-squared values rise to statistically significant levels at periodicities of about 12.5 and 8 hours, indicating a cross-shelf similarity in semi-diurnal and some of the shallow-water tidal constituents. It is not clear why coherence-squared values are not equally high in diurnal periods, un-

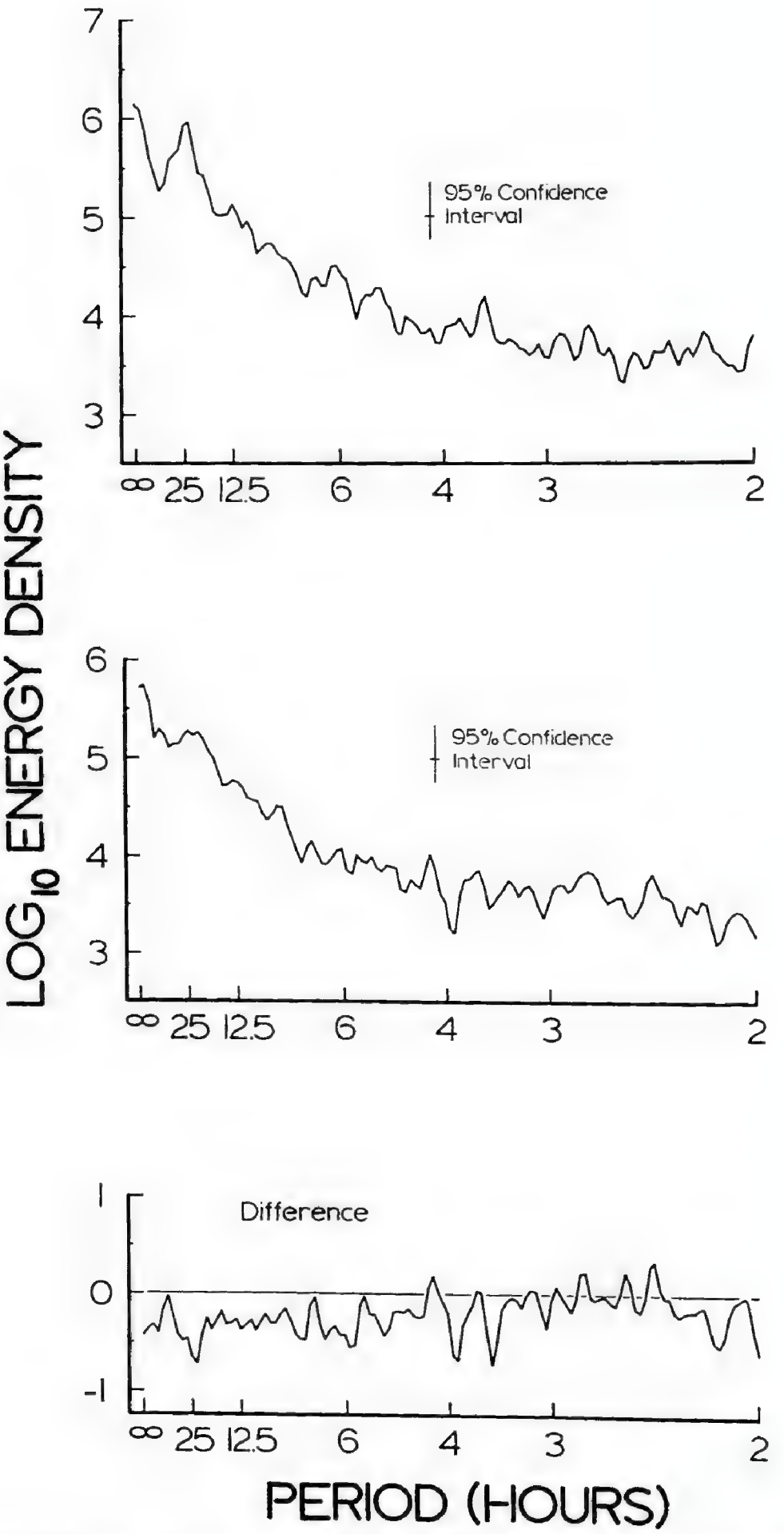

FIG. 4. Energy density spectra of cross-shelf component motion recorded by the top current meters at both the inner and outer stations, 22 March through 26 April 1977. Spectral resolution is 0.004 cycle/hour (c/h). Positive values indicate higher energy density levels at the inner station.

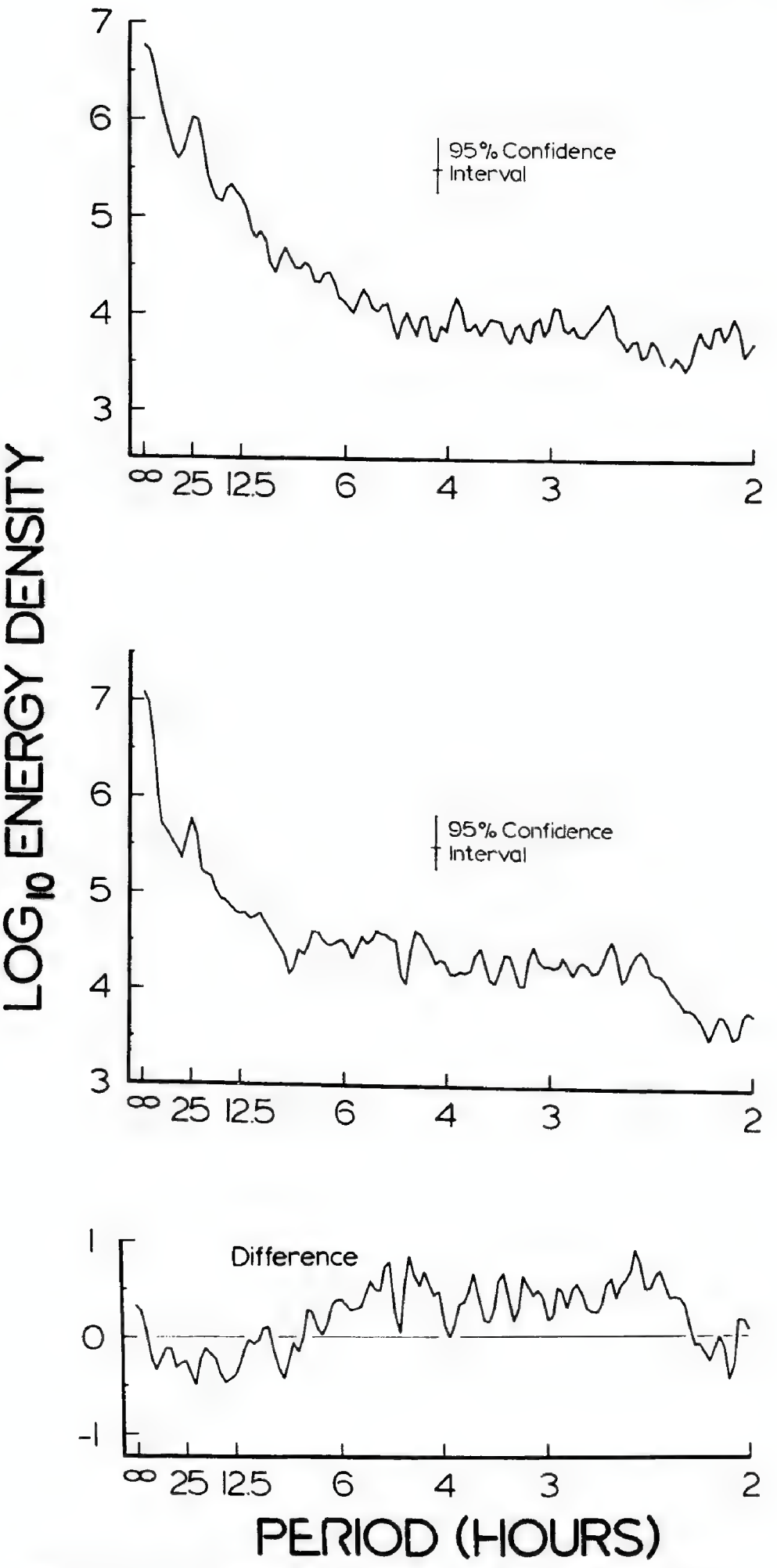

FIG. 5. Same as Fig. 4, but for longshore component motion

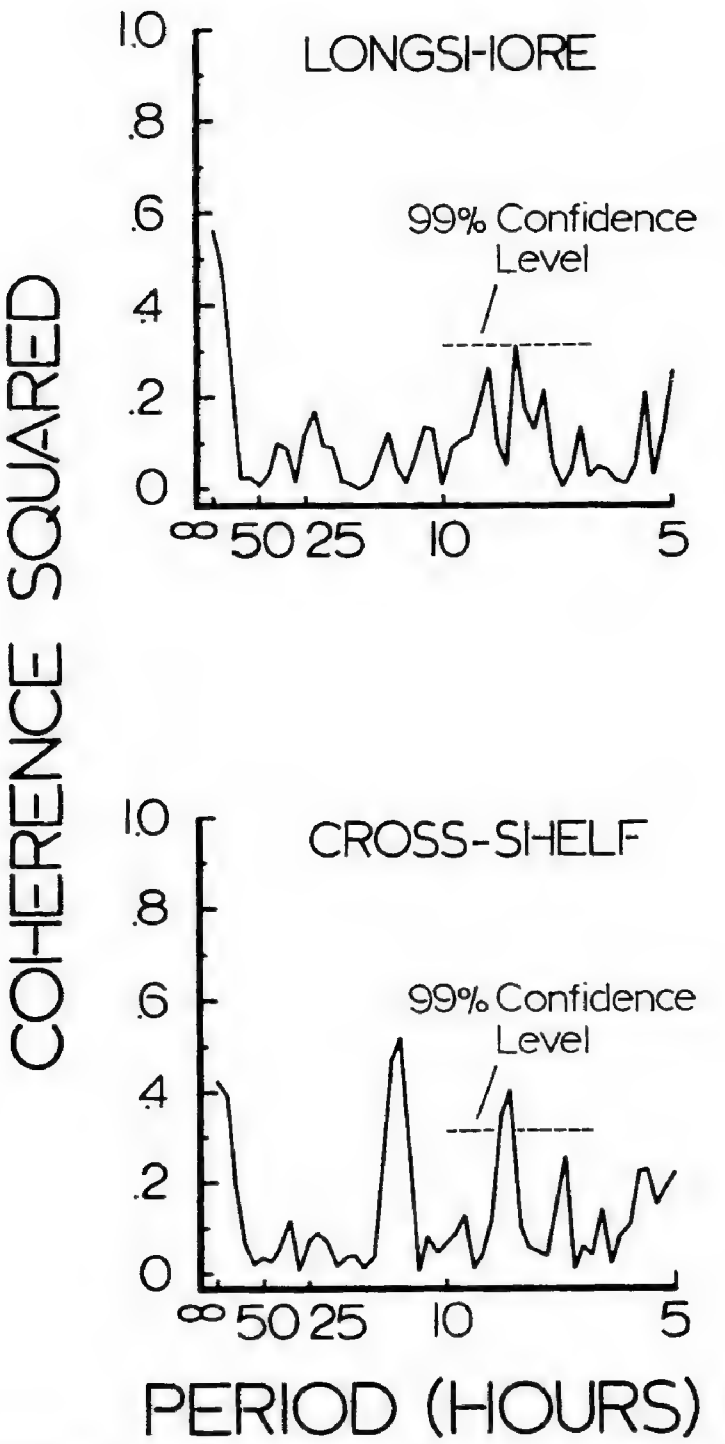

FIG. 6. Coherence-squared spectra for longshore and cross-shelf component motion recorded at the top levels at the inner and outer stations, 22 March through 26 April 1977. Spectral resolution is 0.004 c/h.

less inertial motion at the outer station (period of 25.8 hours) is contaminating that part of the spectrum significantly and destroying the similarity of these motions across the shelf.

Tidal harmonic constants computed from the longshore and cross-shelf components of the two current records (Dennis and Long 1971) are useful for comparing and contrasting this form of rotary motion in inner and mid shelf waters. Table 1 summarizes the harmonic constants for the principal tidal constituents. The pattern that emerges can be seen most clearly in the values computed from the cross-shelf current components. Without exception, larger amplitudes are computed from the offshore current record. Both the diurnal period constituents and the semi-diurnal M_2 constituent have amplitudes approximately twice as

TABLE 1

Harmonic constants of the principal tidal constituents computed from longshore and cross-shelf current components, recorded 28 March through 25 April 1977. Amplitudes in cm/sec, local phase angles in degrees.

INNER STATION		K_1	O_1	M_2	S_2
Longshore	Amplitude	5.3	1.1	0.68	0.53
	Phase	196	188	41	26
Cross-Shelf	Amplitude	2.3	0.8	0.84	0.45
	Phase	321	108	181	147
OUTER STATION					
Longshore	Amplitude	3.7	3.6	0.87	0.76
	Phase	246	239	121	111
Cross-shelf	Amplitude	4.6	1.7	1.69	0.48
	Phase	318	205	227	143

great at the outer study site. The pattern is less clear in the longshore current components; the K_1 constituent has a higher amplitude at the inner station. All amplitudes listed in Table 1 must be interpreted with caution in view of the accuracy of the current meter measurements.

One characteristic of inner shelf waters in general, and of the CBL in particular, is a greater responsiveness to overlying windstress. To investigate this feature in Texas shelf waters, wind data from Port Aransas, Texas, were used to compute coherence-squared spectra. The longshore component of the windstress was compared with the longshore component of the current vector. Results are shown in Figure 7. At the outer station, there is very low coherence between longshore winds and longshore motion over time scales in excess of about five days. Over time scales between approximately one-half and five days, however, coherence-squared values are generally statistically significant at the 95% confidence level. At the inner station, on the other hand, there appears to be a close coupling between longshore windstress and longshore motion at the longest time scales, but not within the 2–5 day periodicities often associated with meteorological forcing. Energy density spectra computed from longshore and cross-shelf windstress components are not shown, as the energy density values deviated only slightly from an exponential decrease with decreasing period. It is noteworthy, however, that this exponential decrease in energy density levels starts at time scales of around 80–100 hours. Values are uniformly high at periodicities in excess of 4–5 days.

DISCUSSION

It is appropriate to note that this study revealed current patterns that fall nicely within the annual cycle that has been compiled from previous studies conducted off the central Texas Gulf coast throughout the year. Earlier studies were based upon results of single current meters moored over the inner shelf. Results presented here suggest that this pattern may involve both inner and mid shelf waters.

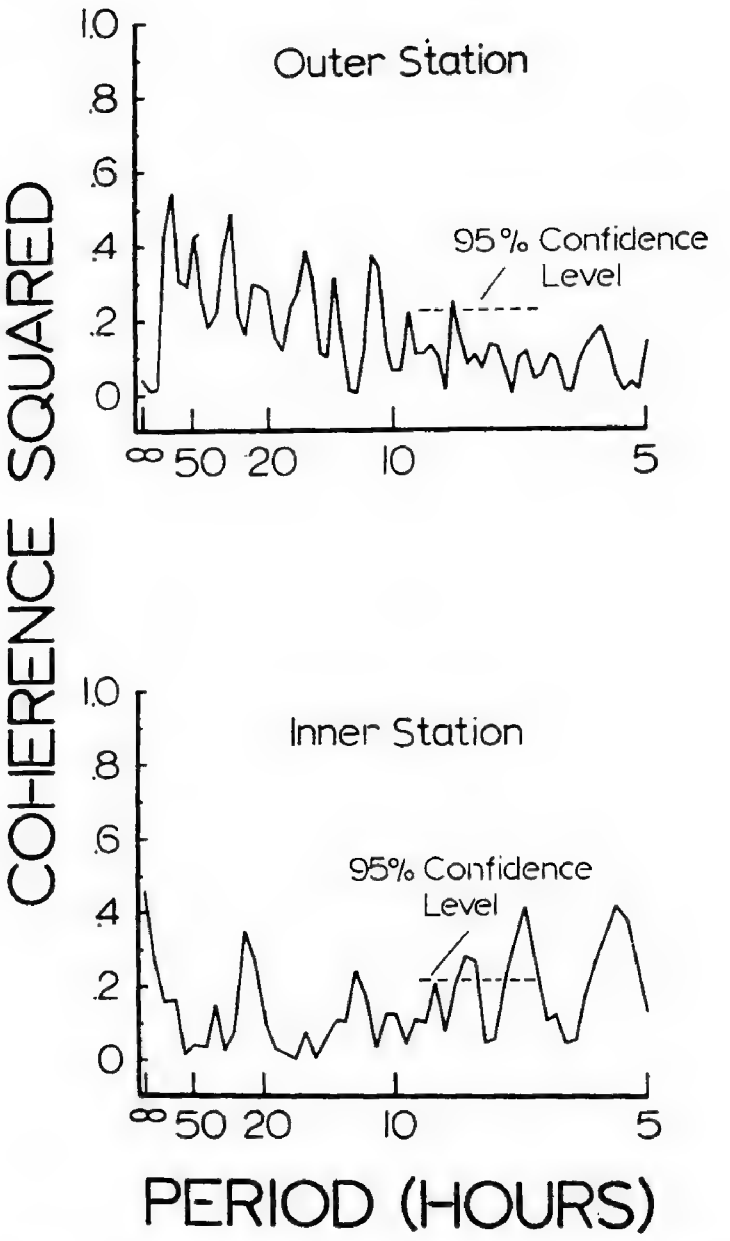

FIG. 7. Coherence-squared spectra between longshore windstress components and longshore current components at the inner and outer stations, 22 March through 26 April 1977. Spectral resolution is 0.004 c/h.

The data obtained in this study provide a rather clear distinction between inner and mid shelf waters, however, in terms of the characteristics of the current itself, and in terms of its response to variations in overlying windstress. As might be expected, cross-shelf variations in the cross-shelf component of the current arise from the presence of the adjacent coast—an application of the kinematic boundary condition. Spectral analysis of the longshore component current data indicates that there is a further dependence upon the time scale over which the motion occurs. Specifically, there is a consistently low coherence between the longshore component of the windstress and the longshore motion at the outer station for time periods greater than about five days. Yet it is over these time scales that the longshore windstress is most coherent with longshore motion at the inner station. The impression created by the data is that over the middle shelf, and presumably beyond, near-surface longshore motion may reflect the effects of larger-scale circulation patterns, which respond to a more regional scale forcing, and which do not extend all the way onto the inner shelf.

Somewhat more puzzling is the lack of coherence in the 2–5 day time scales between longshore motion over the inner shelf and longshore windstress recorded at Port Aransas. One would expect the relatively shallow water column at the inner station to be more responsive to meteorological forcing. The data do not provide a clear-cut answer, but it may be that the surface and benthic boundary layers overlap at such shallow depths, resulting in a more complete and efficient vertical flux of momentum through the entire water column. At the outer station, on the other hand, although the water column is also nearly neutrally stratified, a wind-driven current may decrease exponentially with increasing depth, and windstress effects therefore may be restricted to, and magnified within, a shallower surface layer. If, in fact, wind-driven motions occur through a thicker layer at the inner station, one would then expect a high coherence with windstress events only at the very longest periodicities.

The relative magnitudes of the energy density levels are consistent in a general way with the coherence of near-surface motion with the overlying windstress. It appears from Figures 4 and 5 that energy density levels are highest at locations and over time scales where the longshore component of the current is most coherent with the windstress. At the inner station, low-frequency coupling between longshore windstress components and the longshore motion is statistically significant only over the longest time scales, and it is at these periodicities that energy density values from the nearshore current data are in excess of those from mid shelf waters. Conversely, at the outer station, longshore motion is highly coherent with the longshore component of the windstress at time scales between one-half and about five days, and it is within this range of periodicities that energy levels are consistently higher at the outer station. This general relationship, in turn, is consistent with what one might expect for shelf waters which can be characterized as predominantly wind-driven (Smith 1975, 1978).

The marked offshore deflection that appears in the near-bottom flow at the inner station and in the near-surface flow at the outer station is a feature that does not fit easily into a conceptual model. Cross-shelf transport is not uncommon in this part of the Gulf (Smith 1977, 1979) as elsewhere, but the nature of compensating return flow is not well understood. To the extent that this cross-shelf deflection represents a net mass transport, the compensating motions may have occurred either locally, at some intermediate layer between current meters, or further along the shelf, northeast or southwest of the study area. The possibility of an onshore deflection in the uppermost layers cannot be ruled out, as 58% of the wind directions recorded by the anemometer at Port Aransas during March and April, 1977, were southeasterly or south-southeasterly. Thus, windstress at this time would have had an onshore-directed cross-shelf component. However, the available data are not adequate to resolve this question. It is also unclear why the cross-shelf transport should be confined to the upper part of the water column over the middle shelf, but appear at near-bottom levels over the inner shelf. Greater vertical resolution would be required to establish the existence of a net mass transport or a compensating return flow.

It is appropriate to conclude with an explicit comparison of the CBL in Texas shelf waters and the model that has been constructed from results of previous studies. In view of earlier work, one might expect to find a greater dominance of rotary or oscillatory flow at the diurnal inertial or tidal periodicities at the outer station, 34 km from the coast. This does in fact occur, especially in the cross-shelf component of the current (Fig. 5), although it is not particularly obvious in the PVDs (Figs. 2 and 3). This is most likely because tidal motions in general are poorly developed in shelf waters off the Texas coast. Complete oscillations are recorded only rarely, except during the summer months (Smith 1975), when the net transport upon which tidal motions are superimposed decrease to insignificant values. Thus, during the spring study reported here, there was essentially "straightline flow" recorded at all levels at both stations. The cross-shelf variations in tidal or inertial motions become apparent only through an analysis which isolates these periodicities.

One would also expect the relative importance of kinetic energy contained in the very long period motions to decrease in an offshore direction. This is generally true in Texas coastal waters, however computed energy levels are only slightly lower at the inner station, and only for longshore motions at time scales in excess of about five days. The nontidal motion in mid shelf waters does appear to be appreciably steadier than that recorded over the inner shelf. The PVDs show this qualitatively (Figs. 2 and 3), but they also reveal significant vertical variations at both stations. Indeed, the vertical variations in the timing and the extent of the recorded current reversals appear to be as great as the horizontal variation noted in the near-surface records from the inner and the mid shelf stations. Thus, one must specify clearly the depth at which current records are being compared from study sites within and outside the CBL.

The results of this study support the concept of a CBL-like band running parallel to the central Texas Gulf coast. Although the data are not adequate to define the width of the band, there is sufficient information to characterize it in terms of relatively high values of kinetic energy for very low-frequency longshore motion, relatively greater coupling with overlying wind field at the longest periodicities, and relatively little kinetic energy associated with cross-shelf motion over all time scales.

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TIDAL ANALYSIS AND PREDICTION IN A SOUTH CAROLINA ESTUARY[1]

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ABSTRACT

Tides in estuarine creeks or marsh areas are often difficult to predict using tide tables. When site-specific tidal information is needed for an area remote from primary or secondary reference stations, tidal predictions can easily be generated. We call attention to two available computer programs that can be used to analyze tidal data and accomplish tidal predictions. These programs are obtainable from the National Ocean Survey, NOAA and only require the collection of either 15 or 29 days of hourly spaced tidal data. We illustrate the formulation of tidal statistics and subsequent generation of tidal predictions with data from a tidal creek in North Inlet Estuary, South Carolina. There is close agreement between measured and predicted tides at this location. This technique appears useful in systems with widely different tidal ranges.

INTRODUCTION

Tables for predicted times and heights of high and low waters are published annually (e.g., National Ocean Survey 1979) in the United States and other countries. However, such tables exist for only a certain number of selected areas. Reference locations are often distant from marine laboratories and field sampling sites, and corrections applied to tidal stations with daily predictions are frequently insufficient. In estuarine systems, study sites are commonly located in tidal creeks or high marsh areas which are connected to major inlets by long, meandering creeks. Even when the inlet is in close proximity to a secondary reference station, water levels at remote study areas are difficult to predict. Scientists working in marine systems need accurate tidal information for several reasons. First, characterizing a study area using tidal statistics gives one a better feel for what the physical conditions are at the site, and how they might be incorporated into a study or affect its outcome. Second, the scheduling of biological and other sampling is usually dependent on the tides; e.g., intertidal studies must be done at low tide while the sampling area is exposed. Third, the tidal information itself is often an integral part of research. For example, tidally dependent biological

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rhythms, such as activity patterns, migration and hatching have been demonstrated in marine animals (Enright 1965, Klapow 1976, Christy 1978).

Our purpose in writing this paper is to illustrate how easily tidal predictions may be generated for specific sampling sites. Such predictions would allow investigators to obtain tidal predictions for remote areas where tidal information is unavailable, thus enabling refinement of field sampling schedules as well as providing data relevant to many studies. We will outline how to analyze tidal data and accomplish tidal prediction with illustration on a tidal creek, Clambank Creek, in North Inlet Estuary, South Carolina (Fig. 1). This technique is by no means new and is used routinely by government agencies such as National Ocean Survey, NOAA, to create daily tidal predictions for reference ports. However, it is only seldom that individual investigators have utilized the maze of literature and computer programs to create daily tidal prediction for their particular study site. Our purpose is not to summarize this literature but to call attention to two available programs that can be (1) easily obtained, (2) used on most computers, and (3) used to formulate descriptive tidal statistics and generate tidal predictions. Tidal constituents generated by harmonic analysis of the water-level data we collected, and associated tide prediction curves, are discussed, the intention being to acquaint

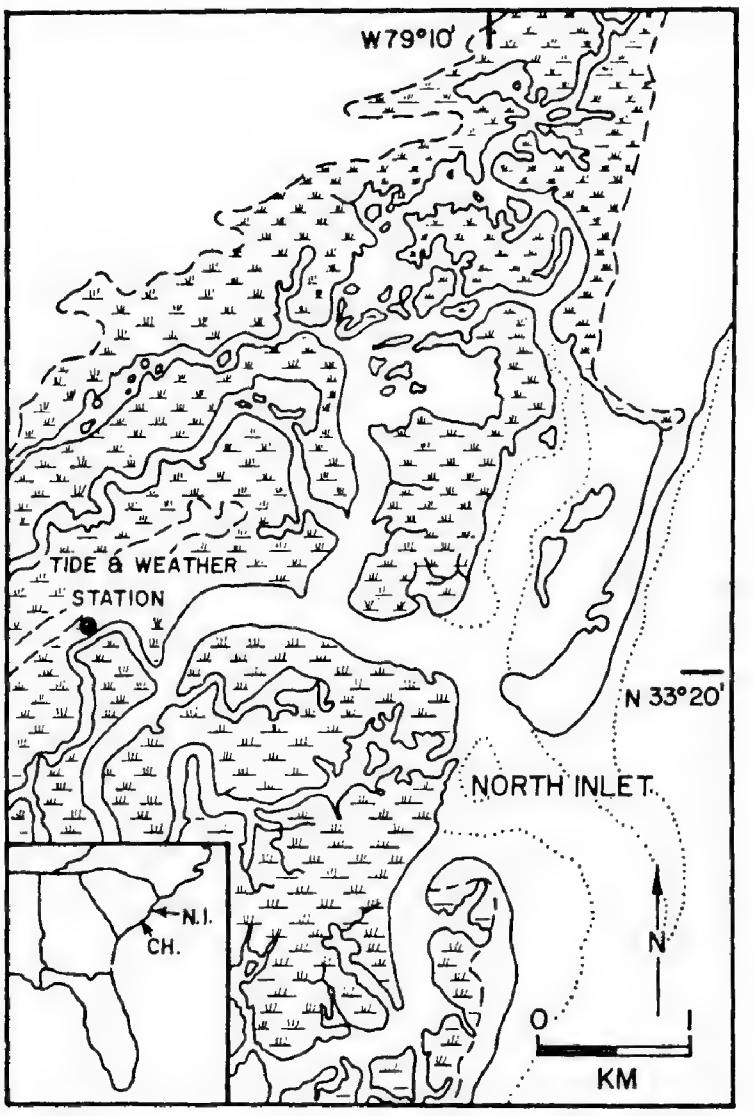

FIG. 1. Area map of North Inlet, South Carolina. Tidal data were collected at the site denoted as tide and weather station

scientists unfamiliar with these programs with the generation of site-specific tidal information.

ANALYSIS AND PREDICTION

Tidal prediction for a particular locality is an empirical determination based on harmonic analysis. The rise and fall of the tide can be expressed by the sum of a series of harmonic terms having certain relations to astronomical conditions (Schureman 1941). Each term represents a hypothetical tide-producing body which is conceived as orbiting the earth and causing a constituent tide with its own period (Marmer 1954). The curves that define each component can be described as oscillations about mean tide level. To separate the constitutents and find their amplitudes and phases, a time series of *in situ* tide height recordings is subjected to least squares fitting by a series of sine and cosine curves (Fourier analysis). The *Curan* program, a FORTRAN-IV program (Dennis and Long 1971), performs the harmonic analysis on either 15 or 29 days of uniformly spaced tidal data. Any computer with a 140K memory which accepts FORTRAN input will execute this program. Minor modifications may be necessary. The end result of this portion of the analysis is amplitude and phase values for the 24 major tidal constituents. Typically, 5 to 7 of these components make up more than 95% of the tidal response. The 24 constituent amplitudes and phases are used to predict the height of the tide at any time.

Curan uses standard Fourier analysis described by Schureman (1941) and entails three basic processes: 1) initial separation of the tidal constituents from the data, 2) orientation of the constituent tides with the astronomical elements, and 3) elimination from each constituent sought, the effects of other tidal constituents (Dennis and Long 1971). Input may be via punched cards or magnetic tape, and the preferred sample rate is one data point per hour. In addition to water level data, *Curan* can also be used for harmonic analysis of vectoral current data. Using the tidal constituents obtained from the *Curan* program, tidal predictions are accomplished with a FORTRAN program described by Pore and Cummings (1967). In addition to the coefficients from *Curan*, this program uses a series of 1025 cosine values, 37 constituent speed values, and pairs of amplitude modification factors and Greenwich equilibrium arguments, found in Tables 14 and 15 of Schureman (1941), corresponding to each tidal constitutent. The sea level datum used for prediction is set by the programmer and usually represents mean sea level. However, mean sea level may vary seasonally due to periodicities in meterorological processes. For example, in the southeastern U.S., mean sea level is greatest in the fall and lowest in late winter due to seasonal atmospheric phenomena. The seasonal sea level cycle can be incorporated into the predictions generated by these programs because the user has the ability to set datum planes. To estimate the magnitude of seasonal sea level changes, the user should consult the *Permanent Service for Mean Sea Level* (1977). The time period and type of output for the *Curan* program can be specified as hourly tidal heights or as the time and height of high and low tide.

CLAMBANK TIDE

The tide in Clambank Creek, North Inlet Estuary, South Carolina (Fig. 1) was measured from July 1974 through May 1975 with an F555 WeatherMeasure water level recorder. Six 29-day tide records were digitized and subjected to harmonic analysis. The eight tidal constituents with the greatest amplitudes from the 29-day series in May, 1975 are presented in Table 1. The tide in Clambank Creek can be thought of as being made up of these component tides, each with a fixed period corresponding to its appropriate hypothetical tide-producing body. For example, the principal lunar component (M_2) is a semidiurnal component with a period of 12 hours 27 minutes. Since the moon's distance from the earth is not constant, the moon's tide-producing force varies. It is greatest at perigee, which

TABLE 1

Harmonic constants calculated for Clambank Creek, North Inlet Estuary, South Carolina, based on a 29-day time series, 1–29 May 1975.

Name of partial tide	Symbol	Amplitude (cm)	Epoch[1] (°)	Period[2]	Theoretical Coefficient Ratio[3]
Semidiurnal components					
Principal lunar	M_2	62.0	226	12.42	100.0
Principal solar	S_2	9.1	290	12.00	46.6
Larger lunar elliptic	N_2	23.2	224	12.66	19.2
Luni-solar	K_2	2.5	290	11.97	12.7
Smaller lunar elliptic	L_2	1.7	227	12.19	2.8
Diurnal components					
Luni-solar	K_1	10.2	123	23.93	58.4
Principal lunar	O_1	7.4	151	25.82	41.5
Principal solar	P_1	3.4	123	24.07	19.4

[1]Corrected to Greenwich meridian

[2,3]From Defant (1960, Vol. 2, p. 267)

occurs every 27.3 days. The larger lunar elliptic component (N_2) is introduced to account for this difference. Diurnal components are also necessary in describing the Clambank Creek tides. The constants K_1 and O_1 are introduced to account for the changing declinations of the sun's and moon's orbits, respectively, to the plane of the equator. Thus each component accounts for some portion of the total tide-producing force.

The amplitudes and epochs for the major tidal constituents were used to compute certain descriptive tidal statistics, e.g., neap and spring range, which characterize the tides (see Marmer 1954). A summary of these statistics for the May series is presented in Table 2. The Form Number (F) represents the amplitude ratio of the principal diurnal component (K_1 and O_1) to the principal semidiurnal components (M_2 and S_2). Where $(K_1 + O_1) / (M_2 + S_2)$ is less than or equal to 0.25, the tide is classed as semidurnal. For all six 29-day intervals we examined, the Form Number for Clambank was 0.25. The relative importance of the constituents varies somewhat from month to month. This may be due to a daily heating cycle and random weather events. If the tidal wave were purely semidiurnal, the two high waters each day would be of equal height, as would the two low waters. However, differences exist in the tidal heights. Whether the effect is primarily in the high or low waters is determined by a phase relationship $D = | M_2^\circ - (K_1^\circ + O_1^\circ) |$, which is to be subtracted from 360° if greater than 180°. Following Marmer (1954), $D = 0°$ implies that the inequality occurs only in the high waters; for $D = 90°$, the inequality occurs both in high and low waters; and for $D = 180°$, the inequality is only the low waters. In the case of Clambank Creek,

TABLE 2

Summary of Clambank, North Inlet Estuary, South Carolina, tide statistics based on the harmonic constants from the 29-day time series record, 1–29 May, 1975.

Parameter	Formula	Value	Interpretation
Form Number	$(K_1 + O_1)/(M_2 + S_2)$	0.25	Semidiurnal tide
Inequality Phase Relationship	$\lvert M_2^\circ - (K_1^\circ + O_1^\circ)\rvert$	48°	Diurnal inequality predominantly in high waters
Phase Age	$0.98(S_2 - M_2)$	63 hrs	Spring tide occurs 63 hrs after new or full moon
Mean Range	$2.2(M_2)$	136 cm	Average tidal range (semidiurnal and diurnal)
Spring Range	$2.0(M_2 + S_2)$	142 cm	Average range during spring tide (semi-diurnal tide)
Neap Range	$2.0(M_2 - S_2)$	106 cm	Average range during neap tide (semidiurnal)
Tropic Range	$2.0(K_1 + O_1)$	35 cm	Average range during tropic tide (diurnal tide); moon at maximum northern or southern declination
Equatorial Range	$2.0(K_1 - O_1)$	6 cm	Average range during equatorial tide (diurnal tide); moon above equator
Diurnal Age	$0.91(K_1 - O_1)$	71 hrs	Tropic tide occurs 71 hrs after the moon's maximum semimonthly declination

D = 48°, implying that the inequality is predominantly exhibited in the high waters.

There is usually a lag of some hours between the time of the astronomical condition tending to produce a maximum tide and the actual maximum as it occurs in nature. The phase age in Table 2 refers to the phase inequality manifested by a variation in the range of the tide, which tends to increase at times of new and full moon. The phase age is the time required for the constituents M_2 and S_2 to arrive at phase agreement, i.e., at maximum range or spring tide. At Clambank Creek we find that spring tides come, on the average, 63 hours or about 2.5 days after full or new moon. For semidiurnal tides in which M_2 is the predominating constituent, the mean range is 2.2 times the amplitude of M_2. At Clambank Creek the mean range is 136 cm. The spring tide range, $2(M_2 + S_2)$, is 142 cm, and the neap tide range, $2(M_2 - S_2)$, is 106 cm. Although the diurnal effects in the North Inlet area are small, we similarly computed maximum (tropic) and minimum (equatorial) diurnal tide ranges. The values are given in Table 2.

The amplitude and epoch values for Clambank Creek were entered into the FORTRAN program of Pore and Cummings (1967), generating the prediction of hourly tidal height values and times and heights of high and low water. The agreement between measured and predicted tides for November 1–4, 1978 is shown in Figure 2. The prediction is based on 29 days of hourly tidal data collected in 1975. The two curves are in close agreement, even though data collected in 1975 were used to predict curves three years later. The mean tidal range predicted (1.61 m) is within 2% of the observed tidal range (1.58 m). Furthermore, comparing 25 days of data, the differences between observed and predicted times and heights of high and low tide are ≤ 1 hour for 96% of the observations and ≤ 30 cm for 98% of the observations. These values are very similar to those used by Swanson (1976) when comparing actual data to that predicted by the tide tables. In Clambank Creek, the tidal range and basin geometry are such that wind effects are usually trivial, and thus present no problems in tide prediction. One would expect meteorological effects to be most pronounced in shallow water or microtidal systems, making it difficult to forecast water level. Kjerfve *et al.* (in press) used this technique to predict the tide at Carrie Bow Cay, Belize, an area characterized by mixed, microtidal tides. Despite potential problems, tides predicted by the *Curan* program were very close to observed tides, and the predictions proved extremely useful. However, systems do exist where meteorological effects are so pronounced that this technique would yield a highly variable output, e.g., Indian River Estuary, Florida (pers. comm., G. Kierspe).

We feel the *Curan* prediction technique is accurate and useful when site-specific tide predictions are needed. NOS uses a similar process to predict tides for primary stations; however, their predictions are generated from many data sets collected over long periods. We certainly do not advocate the technique we have outlined when adequate tidal information is readily available. We are stressing that tides in estuarine creeks or marsh areas often are not easily predicted by

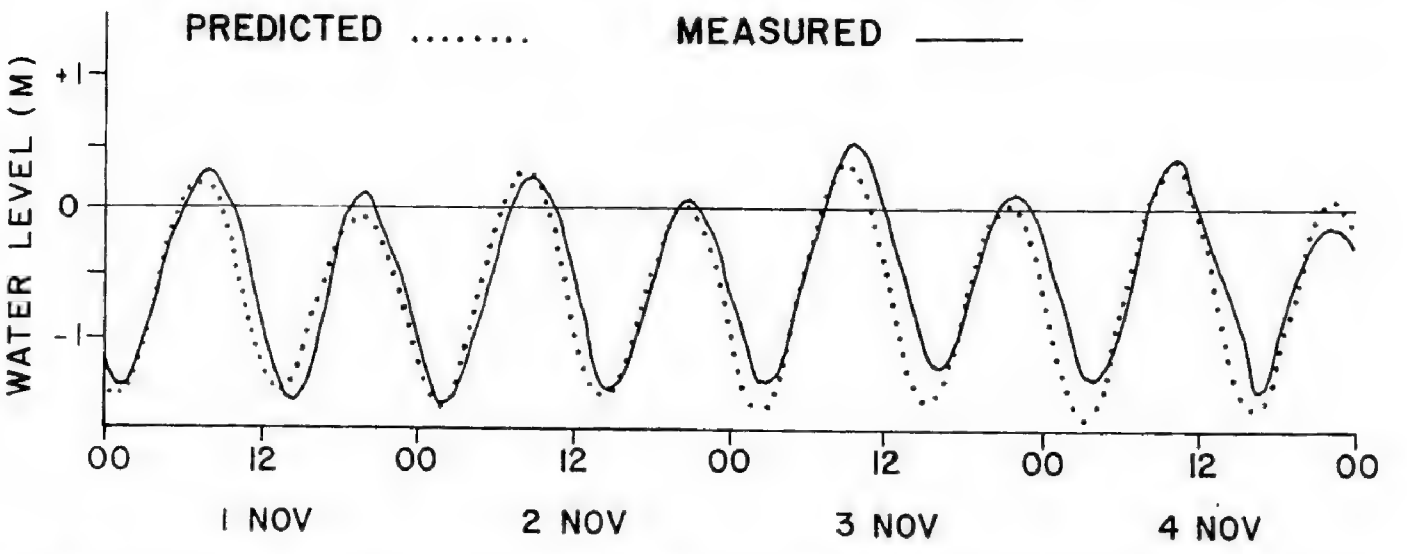

FIG. 2. Comparison of the predicted and measured tide at Clambank Creek for 1–4 November 1978. To accomplish the prediction, the harmonic constants computed on the 1–29 May 1975 tide record were used. Slight deviations between predicted and measured curves are due to non-period meteorological effects.

applying corrections to published tide tables. When this is the case, we contend that the technique outlined can be easily used to create site-specific tidal predictions by collecting less than one month of hourly spaced tide data and subjecting it to harmonic analysis.

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A NATURAL HISTORY OF TEMPERATE WESTERN ATLANTIC FIDDLER CRABS (GENUS *UCA*) WITH REFERENCE TO THEIR IMPACT ON THE SALT MARSH[1]

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ABSTRACT

Fiddler crabs are the most abundant and conspicuous macrofauna in many salt marshes. The study of adaptation to life in the intertidal zone has produced abundant literature on fiddler crab physiology, ecology, and behavior. Most of this literature concerns the three fiddler crabs of the U.S. east coast north of Florida, but general aspects are applicable to other species, especially the many closely related species of the Florida and Gulf coasts. Models of salt marsh ecosystems have not incorporated some of perhaps the most influential effects of fiddler crab biology on marsh structure and function.

This general review emphasizes not only the life histories and survival strategies of temperate western Atlantic fiddler crabs, but also the interaction of these crabs with their environment, and their potential influence on attributes of the whole ecosystem. Feeding and burrowing are especially important in the latter. Many specific aspects of fiddler crab biology are included in the table of contents, and future research is suggested throughout the review. In conclusion, the fiddler crab is considered as a whole system of influences that interacts both positively and negatively with its environment.

INTRODUCTION

Fiddler crabs are ubiquitous in tropical and temperate estuaries around the world. They are believed to have radiated from the equatorial regions outward to higher latitudes, but the longitudinal center of dispersion is argued (see Crane 1975). Of 62 species included by Crane (1975), 43 occur on the coasts of North and South America (30 in one small eastern Pacific area on the Isthmus of Panama), but only three species occur in the temperate western Atlantic. These three species, *Uca pugnax* (mud fiddler crab), *Uca pugilator* (sand fiddler crab), and *Uca minax* (red jointed fiddler crab) account for the greatest macrofaunal biomass in the intertidal salt marsh (Teal 1962, Basan and Frey 1977).

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Perhaps because fiddler crabs are so numerous and conspicuous, they are often included in models of temperate salt marsh ecosystems. In these models, fiddler crabs are represented only as a box within which energy or material is stored before being transferred along a food chain (Teal 1962; Day, Smith, Wagner and Stowe 1973; Wiegert, Christian, Gallagher, Hall, Jones, and Wetzel 1975; Vernberg. McKellar and Vernberg 1978). The activities and byproducts of fiddler crabs can greatly influence transfers of energy or nutrients within an ecosystem, but these effects have not yet been included in the models.

Interest in adaptation to life in the intertidal zone has produced abundant information on the physiology and behavior of intertidal invertebrates. This information was reviewed recently in Bliss and Mantel (1968) and in Newell (1976). Intertidal adaptation is considered necessary for the evolution of invertebrates from sea to land. Fiddler crabs have often been the subject of study on intertidal adaptation.

The recent book by Crane (1975) is the most complete collection of information on fiddler crab taxonomy and behavior to date (see review by Hazlett 1976). Crane only briefly discusses fiddler crab life cycles, their physiology, and the impact of fiddler crabs on their environment because so little is known in general about these areas. Much of the relevant work is the result of extensive study of a few species. The temperate western Atlantic species are frequently studied because they are abundant near east coast laboratories involved in salt marsh ecology.

This review is a general summary of the literature on fiddler crabs, but the major thrust is on physiology, ecology, and the influence of fiddler crabs on their environment. It is directed both to those interested in specific aspects of fiddler crab biology, and to those involved in the study of the ecology of salt marshes. It is limited primarily to the three temperate western Atlantic *Uca* not only because I am most familiar with these, but also because i) the ecology and physiology of these species are so frequently studied, and ii) these crabs are found on both the Gulf and east coasts and are the only *Uca* on the east coast north of Florida. Many of the aspects that are viewed or suggested may be applicable to, or stimulate research on, other less well known species, especially the many closely related *Uca* of the Florida and Gulf coasts. The extensive catalog and bibliography of Gulf crabs by Powers (1977) includes the three temperate western Atlantic fiddler crabs among others, and lists much of the literature of relevance to this review.

Although this is a general review, I have occasionally referred major discussion to authors of other reviews. Space is preserved in this way only when the reviews are recent and readily available, and are on subjects for which I have no further comments and with which I have limited experience. The discussion is also confined at times because little is known of certain aspects of fiddler crab biology, such as nitrogen metabolism and sex ratios. In some of these cases, general discussion, using other organisms as examples, is included to stimulate investigation.

The statements made in this review are frequently the result of distilling into one or several sentences my interpretation of the contributions of several researchers. Most of the studies cited were performed on single populations, at

particular locations and latitudes, and may or may not have been performed in the field.

DISTRIBUTION AND ABUNDANCE

Distribution

Miller (1965) gives an excellent discussion of the distribution of the temperate western Atlantic fiddler crabs. Supporting contributions include those of Teal (1958), Miller and Vernberg (1968), Kerwin (1971), and Whiting and Moshiri (1974). The three species occupy rather distinct zones although some overlap occurs (Aspey 1978). The zones differ in type of substrate, density of plant cover and thus ambient temperatures to some degree (Powers and Cole 1976), soil and water salinity, and soil moisture (Schwartz and Safir 1915, Miller 1965). *U. pugnax* is generally found in cooler muddier areas from the creekbanks to the transitional marsh between muddy and sandy substrates (as defined by Basan and Frey 1977). The area between the levee formed at creek's edge and the transitional marsh (called the back levee meadow marsh by Basan and Frey 1977) consists of muddy substrate and nearly monospecific stands of *Spartina alterniflora*. It is the largest intertidal marsh zone on the Georgia coast (Basan and Frey 1977, Edwards and Frey 1977). *U. pugnax* accounts for the most macrofaunal biomass in this zone (Basan and Frey 1977).

U. pugilator occurs in great number from the transitional areas into the warmer, drier and sandier soils of both the high marsh and the salt flats or barrens. It is well equipped for this environment. It tolerates high temperature and desiccation better than *U. pugnax* (Miller 1965; Teal 1958, 1959; Schwartz and Safir 1915). Its mouthparts are adapted for scrubbing sand grains for organic matter, whereas those of *U. pugnax* are more fit for muddy substrate (Miller 1961, 1965). *U. pugilator* is also found on the sandier creekbanks in Georgia (Teal 1958) and on sandy beaches throughout the east coast (Williams 1965, Miller 1961, 1965). Even on some very muddy creekbanks in Georgia, I have repeatedly collected *U. pugilator* alongside *U. pugnax*.

U. minax prefers lower salinities than either of the above species (Teal 1958, Miller 1965). Studies of the distribution of *U. minax* have been relatively few. Notable articles include those of Gray (1942), Kerwin (1971), and Whiting and Moshiri (1974). Because of a preference for lower salinities, *U. minax* are found on several types of substrate that are inundated with fresher water (e.g., *Juncus* marsh, freshwater or brackish water tidal marshes). In August 1977 I saw *U. minax* in large number ($> 100 \cdot m^{-2}$) on the banks of the Altamaha River, Georgia. The crabs occur inland at least seven miles where salt water intrusion is rare. Kerwin (1971), however, found no *U. minax* burrows in fresh or slightly brackish waters in Virginia.

Fiddler crabs are not distributed uniformly within their respective marsh zones. In general *U. pugnax* density decreases from the levee to the high marsh (Teal 1958, Krebs and Valiela 1978). The younger individuals are generally found nearer the creekbanks (Krebs and Valiela 1978). *U. pugilator* occurs in dense

aggregations often called herds or droves, which wander over a large feeding area usually on beaches or in the sand barrens of the upper reaches of marshes (Crane 1975, Burkenroad 1947, Knopf 1966, Herrnkind 1968c). In locations with greater plant cover, *U. pugilator* feeds in a more dispersed manner. It may feed in one area and burrow in another (Teal 1958). *U. pugnax* and *U. minax* routinely feed individually, though looosely coordinated movement in groups can occasionally be observed. Although Schwartz and Safir (1915) state that *U. pugnax* does not wander far from its burrow while feeding, I have observed masses of *U. pugnax* in areas of the marsh that were not suitable for burrowing because of dense root mats. The nearest *U. pugnax* burrows were perhaps 20 meters away. *U. minax* is patchily distributed with mean burrow densities of 12 per square meter and a range of 0 to 76 per square meter (Kerwin 1971). Salinity differences alone do not account for this variance. Miller (1965) suggests that temperature considerably influences the distribution of *Uca* both locally and regionally. Root mat density greatly affects *U. pugnax* burrow density (Ringold 1979). Interspecific competition may also be influential.

Abundance

The biomass of fiddler crabs is the greatest of all macroheterotrophs in the intertidal salt marshes of the temperate western Atlantic. Krebs and Valiela (1978) estimated the standing stock of all sizes of *U. pugnax* to be 29 ± gm · m^{-2} (dry weight). This value is 22 to 42% greater than that found by Teal (1962) or by Wolf *et al.* (1975). Improved sampling technique was suggested as the cause of this increase, though other sources of variability were not considered.

Published estimates of the densities of *U. pugnax*, *U. pugilator*, and *U. minax* are summarized in Table 1. The seven estimates for *U. pugnax* range from 27 to 152 fiddler crabs per square meter. Unless a sampling program is designed specifically to collect the smaller crabs (< .5 cm), they will usually be missed. Wolf *et al.* (1975) found 92 juvenile crabs (< .5 cm) per square meter in addition to the 113 reported in Table 1. Krebs and Valiela (1978) found 300 to 500 of these juveniles per square meter in August 1972 but only about 30 per square meter in September 1972. Evidently density estimates of fiddler crabs depend not only on sampling technique, but also on spatial and temporal considerations.

LIFE HISTORY CONSIDERATIONS

Life Cycle

Copulation is the culmination of an intricate courtship display in which males wave their large chelae and produce various acoustical signals near a defended burrow (Pearse 1912, 1914a, 1914b; Schwartz and Safir 1915; Crane 1943, 1957, 1975; Salmon and Atsaides 1968). Presumably most *Uca* copulate in their burrows as assumed by Gray (1942) for *U. minax* and by Christy (1978) for *U. pugilator*. However, observations of mating on the surface have been made in the field for about one-third of the known *Uca* species (Altevogt 1959; Crane 1975, pp.

TABLE 1

Density estimates for temperate *Uca* greater than 5 mm carapace width, with investigator, collection site, and area sampled. N = number per square meter.

Species	Nm^{-2}	Investigator	Collection Site	Plot size, No. Plots
U. pugnax	27	Teal (1958)	Low marsh, Sapelo Is., Ga.	.2 m^2 , ?
U. pugnax	61	Teal (1958)	Levee marsh, Sapelo Is., Ga.	.2 m^2 , ?
U. pugnax	84	Basan & Frey (1977)	Low marsh, Blackbeard Crk., Ga.	1 m^2 , ?
U. pugnax	111	Basan & Frey (1977)	Levee marsh, Blackbeard Crk., Ga.	1 m^2 , ?
U. pugnax	110	Krebs & Valiela (1978)	Levee marsh, Great Sippewissett, Mass.	.25m^2 ,32
U. pugnax	152	Ward, Howes and Ludwig (1976)	Levee marsh, Great Bay, N.J.	.52m^2 ,35
U. pugnax	113	Wolf, Shanholtzer & Reimold (1975)	Duplin Estuary marsh, Ga.	1 m^2 ,76
U. pugilator	43	Teal (1958)	*Salicornia-Distichlis* marsh, Sapelo Is.,Ga.	.2 m^2 , ?
U. pugilator	52	Teal (1958)	Creekbank, Sapelo Is., Ga.	.2 m^2 , ?
U. pugilator	41	Hockett & Kritzler (1972)	Beach sand spit, Wakulla Co., Fla.	1 m^2 ,85
U. minax	32	Teal (1958)	"*Minax* marsh", Sapelo Is., Ga.	.2 m^2 , ?
U. minax	12*	Kerwin (1971)	Poropotank River Estuary, Va.	1 m^2 ,125

* (12 burrows) No estimate of the number of crabs this represents was given by Kerwin.

500–504). Temperate species have been observed both in courting and copulating at the surface at night (Burkenroad 1947; Salmon and Atsaides 1968; Crane 1975, p. 520). Nocturnal courtship activity in temperate fiddler crabs is believed to compensate for shorter breeding seasons in temperate zones (Salmon and Atsaides 1968); such activity is not common among tropical *Uca* (Crane 1975, pp. 444, 502).

Semimonthly cycles of reproductive activity are timed to release larvae during neap tides in tropical *U. pugilator* (Christy 1978) and during spring and neap tides in temperate *U. pugnax* (Wheeler 1978). In both cases such timing may increase the transport of larvae into the estuary to appropriate sites for settlement (Christy 1978, Wheeler 1978).

Brood development requires 11 to 13 days and females perhaps adjust the time of copulation or oviposition to better synchronize larval release (Christy 1978). Eggs remain attached to female pleopods forming a mass called a sponge. *U. minax* sponges contain 10,000 to 300,000 eggs (Gray 1942), and *U. pugnax* sponges contain 4,500 to 23,700 eggs (Shanholtzer 1973, Krebs and Valiela in prep.). The number of eggs per sponge depends on the size of the female (Krebs and Valiela in prep., Gray 1942, Gibbs 1974).

Ovigerous females are present during the warm months of the year. Nearer the northern limits of *Uca* distribution (Cape Cod) ovigerous females are found from July through August. This period is longer in more southern marshes (Pearse 1912, Hyman 1922, Crane 1943, Williams 1965, Herrnkind 1968a). At least in temperate regions, field collections of gravid females are evidence that not all the neap or spring tides are equally productive of larvae. Evidently *U. pugnax* and *U. minax* have two peak breeding seasons, but *U. pugilator* (at least in nothern marshes) has only one (Gray 1942, Crane 1943, Shanholtzer 1973).

Although Christy (1978) found that gravid females of tropical *U. pugilator* usually incubate their broods in the terminal chambers of the burrows in which they mated, gravid female *Uca* of the temperate region are said to migrate or at least congregate in areas where a source of free water is readily available (Pearse

1912, 1914a, 1914b; Schwartz and Safir 1915; Crane 1943). Gravid fiddler crabs are rarely active, but during evening or nocturnal low tides they will bathe their sponges in available water (Hyman 1920, 1922, Barnwell 1966). After two to three weeks the female releases her larvae into the water, usually at night (Hyman 1920, 1922; Gray 1942; Herrnkind 1968a; Christy 1978). The time required for a female to bear another clutch is unknown but Hyman (1922) states females have several clutches per season.

Temperate western Atlantic *Uca* larvae pass through five zoeal stages and a megalops stage. all of which are aquatic (Hyman 1920, 1922; Herrnkind 1968a). The five zoeal stages last (collectively) anywhere from one week to over a month, depending in part on diet (Hyman 1920, 1922; Christiansen and Yang 1976). Likewise, the megalops stage may last from four days to perhaps one month (Hyman 1920, 1922; Herrnkind 1968a; Christiansen and Yang 1976; Mauroka 1976).

At the end of the megalops stage the larva settles and transforms into the first crab stage. The stimuli for larval settlement are not known. The length of the zoeal stages and the megalops stage may be timed with the occurrence of spring tides to achieve better dispersal within appropriate habitats (Wheeler 1978, Christy 1978).

The first crab stage lasts three to four days, the second lasts four to five days, and the third about a week (Hyman 1920, 1922). Between the third and fifth crab stages (2 to 3 mm carapace width) burrow digging begins (Hyman 1920, 1922; Herrnkind 1968a). Secondary sexual characteristics are detectable at the third to sixth stages (Hyman 1920, 1922; Miller 1969; Feest 1969). Intermolt periods lengthen such that by crab stage 15, ecdysis occurs about every 5 to 10 weeks (Herrnkind 1968b, Krebs and Valiela in prep.). In *U. pugnax* and *U. pugilator* ecdysis presumably continues once or twice per season until death (Krebs and Valiela in prep., Guyselman 1953).

The Molt Cycle

Although little is known about molting from field studies, detailed observations of molting have been made in the laboratory. Molting is easily induced through eyestalk ablation. Limb regeneration has also been studied in the laboratory (Weis 1976). Thus, structural, compositional and biochemical changes during the molt cycle have been described for temperate *Uca* (Kleinholtz and Bourquin 1941, Guyselman 1953, Snyder and Green 1970). The fine structure of the integument and carapace color changes at various stages of the molt cycle have been studied (Green and Neff 1972, Guyselman (1953). Carapace color changes during the molt cycle can be useful for field studies (Guyselman 1953).

Molting is retarded by light, low temperature, extreme salinities and intrusion by crabs or other disturbances (Weis 1976). Ecdysis does not occur at temperatures below 20°C (Passano 1960a, Miller 1965, Miller and Vernberg 1968, Weis 1976).

Maturation and Lifespan

Shanholtzer (1973) used a time series of size-frequency histograms to estimate certain life history characteristics of *U. pugnax*. Maturation takes about one year.

No difference in growth rates occurs between males and females. The average life-span of these crabs estimated from growth rate data is perhaps one to one and a half years (Shanholtzer 1973). From the observations of sizes in the field, sizes given in Rathbun (1918) and Williams (1965), and from an extrapolation of Herrnkind's (1968b) age vs. carapace width curve, I estimate that temperate fiddler crabs rarely live longer than two years, especially considering their many predators (see Pearse 1914b, Schwartz and Safir 1915; Shanholtzer 1973; Ward *et al.* 1976). Mortality of the larger crabs is quite low, however, some *U. pugnax* may live four or more years (Krebs and Valiela in prep.).

Sex Ratios

Sex ratios of fiddler crabs with more males than females have been measured repeatedly in the temperate western Atlantic species and in a Venezuelan species as well (Alcock *in* Pearse 1912; 1914b; Schwartz and Safir 1915; Shanholtzer 1973; Valiela, Babiec, Atherton, Seitzinger and Krebs 1974; Wolf *et al.* 1975; Ahmed 1976). Some workers feel these are due to differential mortality. Females are supposedly more easily caught (Shanholtzer 1973, Wolf *et al.* 1975). There is argument, however ,whether or not differential mortality can account for sex ratios deviating from 1:1 (see Shaw and Mohler 1953; Kolman 1960; Emlen 1968a, 1968b; Leigh 1970; Wenner 1972; Spieth 1974). Sex ratios with more males than females seem at best to occur only transiently or in very special mating systems (Anderson 1961, Hamilton 1967). The mating system of *Uca* is considered promiscuous with territorial males competing for females. Deviations from Fisher's (1930) theoretical 1:1 ratio should favor females in such cases (Willson and Pianka 1963, Emlen 1973).

Although deviations from expected sex ratio seem common for Crustacea (Wenner 1972), perhaps for temperate western fiddler crabs the preponderance of males is an artifact of sample collection. The techniques employed by Wolf *et al.* (1975) and by Shanholtzer (1973) may have biased their results toward male *U. pugnax*. Wolf *et al.* (1975) removed crabs from the surface within a one square meter plot for 20 to 40 minutes. The efficiency of surficial removal was determined by digging twelve similar plots to a depth of one meter. Shanholtzer (1973) collected all of her samples by digging in this manner. Of 76 samples included in the analyses of Wolf *et al.* (1975) only four came from the tall *Spartina* areas.

Surficial removal will bias the sample towards males because females of *U. pugnax* spend more time in their burrows than males (Pearse 1912, 1914b; Schwartz and Safir 1915; Valiela *et al.* 1974). Males spend more time at the surface feeding perhaps to compensate for having only one feeding chela (Valiela *et al.* 1974). Males will often confront a disturbance with a threat posture, but females will generally escape (Crane 1975). With regard to differential mortality, males appear to be more exposed to predators.

Most importantly, samples taken in the medium and short *Spartina* areas during the breeding season will strongly bias samples towards males. Ovigerous females migrate toward damper creek bank areas in the summer, which should

cause an increase in the male-female ratio on a transect inland from the creek bank (Pearse 1912, 1914a, 1914b; Schwartz and Safir 1915; Crane 1943). Thus, until unequivocal data are collected, a 1:1 sex ratio should be assumed.

Predators

Fiddler crabs are consumed by a large number of avian predators including egrets, ibis, herons and other shore birds (Shanholtzer 1973). Clapper rails (*Rallus longirostris*) may rely on *Uca* for 97% of their food (Ferrigno *in* Ward *et al.* 1976). I have observed large numbers of cattle egrets (*Bubulcua ibis*) and snowy egrets (*Leucophoyx thula*) apparently consuming fiddler crabs in the back levee meadow marsh after dawn. Similar observations have been made by Pfeiffer (1974). Ward *et al.* (1976) were unable to demonstrate an increase in fiddler crab standing stock in areas where avian predators were excluded, but migration was not prevented.

Blue crabs (*Callinectes sapidus*) and channel bass (*Sciaenops ocellata*) are common predators of fiddler crabs also (Shanholtzer 1973, personal observation). In addition, raccoon (*Procyon lotor*) feces filled with *Uca* parts can be found on the marsh on most mornings in Georgia.

Additional predators are listed by Shanholtzer (1973) who points out that only a few of all fiddler crabs consumers are permanent marsh inhabitants. Thus fiddler crab predation may represent an energy export from temperate salt marshes.

BEHAVIORAL AND PHYSIOLOGICAL ADAPTATION

The three species of *Uca* that occur in the temperate western Atlantic are intertidal and are well adapted for the fluctuating water levels, salinities and temperatures found in temperate saltwater and brackish tidal marshes. The various adaptations of fiddler crabs to life in the intertidal zone have been of primary importance to physiological ecologists. Indeed most of the literature on *Uca* concerns this subject. Additional information on behavioral adaptations has been reviewed by Crane (1943, 1957, 1975). Physiological adaptations of fiddler crabs and other Crustacea are generously treated by Newell (1970, 1976), the series edited by Bliss and Mantel (1968), and Edney (1960, 1961). Adaptations of temperate fiddler crabs have often been compared to those of tropical fiddler crabs (e.g., Tashian 1956; Demeusy 1957; Vernberg and Tashian 1959; Vernberg 1959a, 1959b; Miller 1965; Vernberg and Costlow 1966; Miller and Vernberg 1968).

Endogenous Rhythms

Daily (24 hr) and tidal (24.8 hr) endogenous rhythms of locomotor activity, oxygen consumption, and color change act together to help the fiddler crab time its alternative marine and terrestrial phases of existence (Fingerman 1957b, Barnwell 1968, Palmer 1973). Temperate *Uca* in areas with semidiurnal tides are most active when the marsh is exposed during daylight, especially during morning

hours (Fingerman 1957a, Barnwell 1966). Fiddler crabs are also especially active when low tides occur after dark (Brown, Bennett and Webb 1954; Bennett, Shriner and Brown 1957; Barnwell 1966, 1968). Oxygen consumption rhythms reflect locomotor activity (Brett, Webb and Brown 1959).

Rhythms of color change tend to darken the crab during daytime low tides (Webb 1976). This may help to disguise it during terrestrial activity (Crane 1944). This rhythm of color change is routinely interrupted in males by blanching during courtship (Crane 1943, 1944). In either sex blanching will also reduce heat gain from insolation (Wilkens and Fingerman 1965, Barnwell 1968, Smith and Miller 1973).

The daily and tidal cycles reinforce one another to produce semilunar (14.8 da) and lunar (29.6 da) cycles (Brown *et al.* 1954). The relative contributions of each of the two cycles to the crabs in the field are difficult to determine. Evidently the daily cycle is somewhat dominant in natural light cycles, especially in the higher marsh areas (Webb and Brown 1965, Barnwell 1968, Webb 1976). The express significance of these rhythms in the field is not well understood.

Courtship and Territorial Displays

The intricate displays of *Uca* have been the devotion of Crane for 35 years. Recently she extensively reviewed the literature (1975). Many displays are administered by the large claw of the male. Since fiddler crabs are primarily active on the surface at low tide, visual and acoustical signals have replaced the chemical communication of aquatic decapods (Bliss 1968, Salmon and Atsaides 1968, Schöne 1968). Hence, the large claw is of great social importance but is not used effectively as a weapon or feeding appendage. In fact, it is cumbersome, inhibits rapid escape and occupies the site of a feeding chela (females have two feeding chelae, males only one).

Acoustical signals are produced in a variety of ways. They often occur in conjunction with visual displays during the day, but they alone are used at night (Salmon 1965, Salmon and Atsaides 1968). Stridulation, vibration or tapping against the carapace or marsh surface, contact with other crabs and respiratory activity account for sixteen sounds described by Crane (1975, pp. 480–485). All of these sounds are believed to have some social significance, but not all are produced by each *Uca* species. Each of the temperate western Atlantic *Uca* produces specific stridulations and each also stamps the substrate (Salmon 1965, Salmon and Atsaides 1968, Crane 1975).

Hard-shelled Copulation

Crane (1975, pp. 500–504) has most recently detailed precopulatory behavior and copulation in *Uca*. In all observations of copulation and intense precopulatory behavior, the female is hard-shelled, unlike aquatic marine decapods. This reduces the chances of desiccation and structural damage during copulation at low tide (Bliss 1968).

Respiration

Semiterrestrial organisms that can metabolize the oxygen in air should have an energetic advantage over competitors that use only the oxygen in seawater (Newell 1976, Edney 1960). Fiddler crabs have gills for deriving oxygen from water as do all Crustacea. When the tide recedes, fiddler crabs carry within their branchial chambers a supply of water that is circulated over their gills. Diffusion of oxygen from the air into this water provides the crab with more oxygen than is available to submerged animals. Evaporative cooling and the process of feeding cause this water to be gradually lost. Frequent trips to moist burrows prevent desiccation (Wilkens and Fingerman 1965, Smith and Miller 1973, Powers and Cole 1976).

While in their burrows at high tide, metabolic requirements are low, burrow oxygen is low, and crabs metabolize anaerobically (Barnwell 1968, Teal and Carey 1967). Since low marsh zones are inundated longer than upper zones, daily respiration rates will vary with elevation (Barnwell 1968, Newell 1973).

The respiration rate of the temperate *Uca* has been measured by many investigators. Various exogenous and endogenous factors affect fiddler crab respiration, so the reported rates vary. Maximum rates for *U. pugnax* are about 550 to 600 μl $O_2 \cdot g\ (DW)^{-1} \cdot hr^{-1}$ at about 40°C (Edwards 1950; Tashian 1956; Vernberg 1959a, 1959b; Teal 1959; Shanholtzer 1973). Oxygen use for *U. pugilator* and *U. minax* is similar to that of *U. pugnax* though rates vary with temperature and experiment (e.g., Brown *et al.* 1954, Vernberg 1959a, Teal 1959).

Measurements of respiration rates at various ambient temperatures show variable Q_{10}'s for both *U. pugnax* and *U. pugilator* (Vernberg 1959a, Teal 1959). At low temperature ranges Q_{10}'s are highest (as much as 5.8 for *U. pugilator* in Vernberg 1959a). Between 15°C and 40°C, Q_{10}'s are 1.5 to 2.5. Metabolic acclimation to warm and cold temperatures has been repeatedly demonstrated for temperate western Atlantic *Uca* except *U. minax* (*e.g.*, Teal 1959; Vernberg and Tashian 1959; Vernberg 1959b; Turpin, Van Winkle and Mangum 1970; Dame and Vernberg 1973). Acclimation is controlled by an eyestalk hormone (Silverthorn 1973). Acclimation to temperature will cause respiration rate to vary with the previous temperature regime in *U. pugnax* and *U. pugilator* (Dame and Vernberg 1973).

The rate of oxygen use varies considerably with activity in many invertebrates. Fiddler crab activity varies with tide, time of low tide, period within low tide, elevation of marsh and sex, among other influences (see "Feeding Periods"). Primarily because of long-term temperature differences (Newell 1973), oxygen use varies both with season (Vernberg 1959a; Webb 1972, 1976; Webb and Brown 1961) and with latitude (Edwards 1950; Tashian 1956; Demeusy 1957; Vernberg 1959a, 1959b).

Nitrogen Metabolism

Published data on nitrogen metabolism in *Uca* are lacking, though, as a special problem of adaptation for life in the intertidal zone, nitrogen metabolism in other

semi-terrestrial Crustacea has been explored (Parry 1960, Hartenstein 1968, Gifford 1968). In western Atlantic salt marshes, nitrogen is a major nutrient in critical supply, and is needed by vascular plants, algae and decomposers (Valiela and Teal 1979, Darley, Montague, Plumley, Psalidas and Sage in prep.). Nitrogen excretion by *Uca* may be no less important to the environment in which they live and feed than it is for the environments of other Crustacea such as *Palaemonetes pugio* (Welsh 1975) and *Crangon franciscorum* (Nelson, Simmons and Knight 1979). Aquatic Crustacea produce ammonia as their primary end product of nitrogen metabolism. Most is excreted through the gills (Kaestner 1970) and all is released directly into the surrounding water.

For semiterrestrial fiddler crabs, the advantages and disadvantages of ammonia excretion have been discussed in the literature. Secreting ammonia rather than urea or uric acid saves energy because the formation of the required enzymes, and the formation of urea and uric acid themselves, use ATP not required in ammonia excretion (Hartenstein 1968). On land, however, water, which is believed necessary to remove ammonia, must be conserved to prevent desiccation.

The widespread ammonotelism among semiterrestrial and terrestrial Crustacea is suggested by Parry (1960) as a reason for the relative lack of success of Crustacea on land. Because the more landward Crustacea evidently excrete less nitrogen, Parry (1960) suggested that, rather than produce a less soluble excretory product, these Crustacea reduce their protein metabolism in an effort to reduce the water required to remove ammonia. A land isopod *Oniscus asellus*, however, secretes ammonia as a gas and tolerates high levels of ammonia in its blood (Hartenstein 1968).

Storage of nitrogen, rather than reduced metabolism, can also explain the lower excretion rates of more landward Curstacea. The land crab *Cardisoma quanhumi* stores uric acid; ammonia accounts for only one-third of its nitrogenous products of metabolism (Gifford 1968). Uric acid formation and toleration of large quantities of ammonia in the blood between exposures to water help landward Crustacea conserve water.

Fiddler crabs, which generally have ready sources of water, probably find an energetic advantage in ammonotelism. Whether they also store uric acid, as in *Cardisoma quanhumi*, and how their nitrogenous wastes affect their environment are unknown.

Thermal Death and Molting Limits

The upper thermal death limit for the temperate western Atlantic *Uca* is around 40°C in water-saturated air, and around 45°C in dry air (Teal 1959, Vernberg and Tashian 1959, Wilkens and Fingerman 1965). The difference is caused by the increased effectiveness of evapotranspirative cooling in dry air. The lower thermal death limit is 2–3°C (Vernberg and Tashian 1959) although molting will not occur below 20°C (Passano 1960a, Miller 1965, Weis 1976). Edney (1961, 1962) believes the upper limit is more sharply defined because selective forces were stronger for the upper limit than for the lower limit as *Uca* evolved into the

intertidal zone. Ambient temperatures in most temperate salt marshes seasonally exceed by considerable amounts both upper and lower death limits. Such extremes are avoided by burrowing.

An Optimization Problem

Temperate fiddler crabs in the intertidal zone are subject to temperature stress, variable salinity and desiccation (Newell 1970, 1976; Bliss 1968; Edney 1960, 1961). Evapotranspiration, though it offers the advantage of cooling, increases internal body fluid salinity. This must be counterbalanced physiologically. Evapotranspiration also increases the risk of desiccation, so a ready source of water is required for replenishment. As crabs settle further inland the tradeoff between cooling and desiccation becomes increasingly acute. Evidently the more terrestrial Crustacea conserve water to prevent desiccation, so they must use less water for cooling by evapotranspiration. According to Edney (1960, 1961) this dilemma accounts for the relatively poor success of Crustacea on land.

Solving the Problem

Fiddler crabs are hyper-hypo-osmoregulators (Green, Harsch, Barr and Prosser 1959; Baldwin and Kirschner 1976a, 1976b). Such regulation is under the control of an eyestalk hormone (Heit and Fingerman 1973). Fiddler crabs can survive the fluctuating salinities of salt and brackish tidal marshes (which usually requires hyper-osmotic regulation) and can survive increased internal fluid salinity caused by evapotranspirative cooling (which requires hypo-osmotic regulation).

Since temperate fiddler crabs exist at or outside their lethal temperature limits, they have several adaptations to control body temperature (see especially Smith and Miller 1973, and the discussion by Newell 1976). Because of their long, jointed walking legs, little surface area need be in contact with the substrate. This reduces heat gain via conduction (Newell 1976). Species that inhabit drier and less protected areas are generally more globose (e.g., *U. pugilator*) than those of damper shaded areas (e.g., *U. pugnax*). This reduces heat gain by radiation to some minor degree, and allows a greater storage of water for evapotranspirative cooling. This type of cooling is the most effective way of removing heat from the body while at the surface (Newell 1976). Fiddler crabs most successfully evade overheating by moving into their burrows, or by moving into the shade. However, body temperatures soon return to higher levels upon re-exposure (Smith and Miller 1973). The crabs make frequent return trips to burrows, which allow replenishment of water used for evaporative cooling (Wilkens and Fingerman 1965, Smith and Miller 1973, Powers and Cole 1976).

Fiddler crabs may adjust their body temperature a few degrees by orienting appropriately to the sun or wind (Smith and Miller 1973). Under severe desiccation or insolation they produce "foam baths" that are believed to help regulate body temperature (Altevogt 1968).

In winter, temperate fiddler crabs avoid lethal cold temperatures by burrowing deeply (Gray 1942, Crane 1943). They must begin this hibernation after temperatures drop below 10 or 12°C, the temperature at which locomotor activity is impaired (Miller and Vernberg 1968). Should they not burrow deeply enough they will die (Smith and Miller 1973). During winter in Georgia a few *U. pugnax* and *U. pugilator* can nearly always be found on the surface or just inside open burrows. The soil temperature at which fiddler crabs emerge is not known.

BURROWS

Fiddler crabs are frequent burrowers in temperate western Atlantic marshes. Digging of burrows begins when the crabs are very small (in the third to fifth crab stage, Hyman 1920, 1922; Herrnkind 1968a, 1968b). The digging behavior of fiddler crabs has been amply described (see Pearse 1912, 1914a, 1914b; Schwartz and Safir 1915; Dembowski 1926; Altevogt 1955; Crane 1975). New or existing burrows are excavated on the average of once per day by *U. pugilator* (Knopf 1966, Herrnkind 1968b). Ten sand fiddler crabs (*U. pugilator*) completely turned over the soil in a 0.5 m^2 laboratory plot within one week through burrowing activity (Allen and Curran 1974). In one laboratory experiment *U. pugnax* did not burrow as frequently as *U. pugilator* (Coward, Gerhardt and Crockett 1970). In the field, however, burrow density in *U. pugnax* zones in Georgia was 8 to 10 times greater than that either in nearby *U. pugilator* zones or in areas of species overlap (Aspey 1978).

The density of large fiddler crab burrows varies between 40 and 120 per square meter in the low marsh areas near creekbanks (Krebs and Valiela 1978). Basan and Frey (1977) estimated the density of all burrows to be 700 per square meter (average diameter 6 mm) to 250 per square meter (average diameter 9 mm) from the streamside and levee areas to the back levee meadow marsh.

Root mat density in salt marsh soils greatly influences the frequency of burrowing by *U. pugnax*, but not by *U. minax* (Ringold 1979). Often in soils with very dense root mats, only *U. minax* burrows are found. In such areas, I have found *U. minax* burrows with their entrance ways modified so that only the much smaller *U. pugnax* could enter. Once burrows are excavated in dense root mats they seem to be highly valued and are maintained for years. I artificially burrowed into a dense root mat using a 16 mm auger bit and drill in 1978. These burrows were immediately occupied by *U. pugnax* and have been maintained to present, but screened test tubes inserted into the marsh filled with sediment within one week.

Burrow morphology has been described using plaster, rubber, or epoxy casts. Dembowski (1926) described burrows of *U. pugilator* and Gray (1942) described those of *U. minax*. More recently, and in more detail, the burrows of all three species of temperate western Atlantic *Uca* have been described along with the burrows of other marsh inhabitants (Frey 1970, Allen and Curran 1974, Basan and Frey 1977). Generally, all these *Uca* burrows are nearly vertical and straight, circular in cross-section, unlined, unbranched, and commonly with an enlarged

terminus. Adult *U. minax* burrows are 2.5–3.0 cm in diameter, penetrate 30 to 65 cm or more and may have chimneys or domes. Burrows of adult *U. pugilator* may be L or J-shaped, 1–2 cm in diameter, 10–20 cm deep (although much longer and much shorter burrows exist), and without chimneys. *U. pugnax* burrows are 1–2 cm in diameter, typically 15–25 cm in depth, may be U-shaped, commonly intersect other burrows (those of the crabs *Eurytium limosum* and *Sesarma reticulatum*), and may have chimneys (all descriptions are from Basan and Frey 1977). Apparently the stimulus for burrow closing by *Uca* has not been identified (Crane 1975), although molting crabs are said to plug their burrows (Krebs and Valiela in prep.). Burrows may or may not be plugged on incoming tides.

Burrows allow fiddler crabs to adapt to a semi-terrestrial existence. Powers (1975a) thoroughly discusses the importance of burrows to some nontidal species of *Uca*, and the more general points are also applicable to the temperate western Atlantic *Uca*. Burrows provide relief from both hot and cold ambient temperatures (Gray 1942, Wilkens and Fingerman 1965, Smith and Miller 1973, Whiting and Moshiri (1974, Powers and Cole 1976). They provide a refuge from both aerial and terrestrial predators during exposed periods, and aquatic predators when the marsh is flooded (Pearse 1912, 1914a, 1914b; Schwartz and Safir 1915; Hyman 1922; Crane 1975). Burrows contain water at low tides (Pearse 1914b, Miller and Maurer 1973, Crane 1975, Aspey 1978), and fiddler crabs have been observed to return to them every 10 to 30 minutes while feeding on the exposed marsh surface (Wilkens and Fingerman 1965, Powers and Cole 1976). Apparently this periodic return is to renew respiratory water lost both through evapotranspirative cooling (Smith and Miller 1973, Powers 1975b, Powers and Cole 1976) and through feeding activities (Miller 1961).

Burrows need not contain standing water but must only be damp since at least some *Uca* species can extract moisture from damp sand (Powers 1975a, 1975b). *U. pugilator*, burrowing in the sandy areas of the high intertidal zone, digs to damp sand; their burrows rarely contain standing water. *U. pugnax* and *U. minax* burrows, however, usually contain standing water which seeps through the waterlogged soils.

The burrow is the center of a territory defended both for the protection offered and in courtship (Crane 1975, pp. 510–513). Burrows, and the towers and domes occasionally around *U. pugnax* and *U. minax* burrows, may enhance the effectiveness of acoustical signals made by fiddler crabs during courtship (Salmon and Atsaides 1968). Whether or not temperate fiddler crabs routinely copulate in their burrows is unknown, although *U. pugilator* in a southwest Florida mangrove island was reported to do so (Christy 1978).

Burrows are well suited for molting since i) water is necessary for successful molting (Passano 1960b, Kaestner 1970), ii) freshly molted semiterrestrial crabs are subject to desiccation and to predation (Bliss 1968, Schwartz and Safir 1915), and iii) molting in the presence of disturbance is slowed in fiddler crabs (Weis 1976).

Burrows not only allow *Uca* to exist in the intertidal zone, but also may be important to the marsh ecosystem. Burrows are known to provide a microhabitat for

a community of organisms (Bright and Hogue 1972). They have been shown to aerate marsh soils (Wiedemann 1972, Edwards and Frey 1977). This may not directly affect the growth of the salt marsh cordgrass *Spartina alterniflora* because this plant aerates its own roots with oxygen in excess of that needed for root respiration (Teal and Kanwisher 1966). However, E. L. Dunn and I noticed enhanced growth of *Spartina alterniflora* adjacent to holes made by coring the marsh.

Nitrogen that is excreted by fiddler crabs within burrows should be readily available to adjacent plant roots. The frequency of burrowing and the subsequent turnover of soil (Edwards and Frey 1977, Basan and Frey 1977) may enhance growth of *Spartina* or provide outlets for gases produced by anaerobic soil microbes. In addition, burrowing may bring bits of root and rhizome to the surface, which would provide another mechanism for organic matter to enter the marsh-estuarine ecosystem (de la Cruz and Hackney 1977). Excavating organic matter from the anaerobic soils below ground to the more aerobic surface allows degradation of organic matter that would otherwise accumulate as peat. In addition, excavated organic matter that decays at the surface should provide more food for fiddler crabs.

FEEDING

Food Processing

Miller (1961) meticulously described the intricate feeding mechanism of temperate western Atlantic *Uca*. Bits of mud or sand are scooped from the marsh surface with the small chela and transported to the mouthparts. The mouthparts of *U. pugilator* are better able to scrub sand grains than those of either *U. pugnax* or *U. minax* which are adapted for feeding in mud (Miller 1965).

The mouthparts scrub organic material from the larger sand grains. The lighter material of greater organic content floats upward toward the buccal cavity in water drawn from the branchial chambers. The heavier more inorganic materials tends to drool down the outside of the antero-ventral surface below the mouthparts. It is periodically scraped away by a feeding chela and the little ball of matter that results is deposited on the marsh surface. These balls are easily distinguished from fecal pellets; they are more spherical, lighter in color, and composed of coarser material. They contain less organic matter than the marsh surface, whereas fecal pellets contain more than the marsh surface (Altevogt 1956, Valiela *et al.* 1974).

Food entering the buccal cavity goes to the cardiac stomach after passing through a short esophagus. Stomach contents contain both organic and inorganic material (Shanholtzer 1973; Schwartz and Safir 1915; Pearse 1912, 1914a, 1914b). While in the cardiac stomach, the contents are attacked by various enzymes from the hepatopancreas (Kaestner 1970; Van Weel 1970; Marshall and Orr 1960; Eisen and Jeffrey 1969; Eisen, Henderson, Jeffrey and Bradshaw 1973). The food-enzyme slurry is then masticated in a well developed gastric mill (Miller 1961) before passing into the pyloric stomach. The intricate filtering system of the pyloric stomach of decapods has been described by Marshall and Orr

(1960) and by Kaestner (1970, Ch. 10). Tiny particles and liquid organics pass through this filter into the hepatopancreas where digestion and absorption are completed (Van Weel 1970). Particles not passing through the filter are directed to the hindgut. As the waste material enters the hindgut, coarser particles are formed into a rod around which finer particles are pressed. This results in rod-shaped fecal pellets with a coarse center surrounded by fine particles, all wrapped in a mucus membrane (Kraeuter and Haven 1970, Altevogt 1956, Moore 1932).

In areas where fiddler crabs feed, the marsh is littered with fecal pellets and the balls of rejected material. Fecal pellets survive rainfall and tidal inundation and are washed into slight depressions in great numbers. The balls of rejected material are destroyed by inundation (Basan and Frey 1977, Edwards and Frey 1977).

Food Sources

According to Marshall and Orr (1960), most Crustacea are omnivorous. The temperate western Atlantic fiddler crabs are no exception. They ingest organic particles that are available on the moist marsh surface (Pearse 1914b). Analysis of the cardiac stomach contents of 13 *U. pugnax* revealed particles consisting of one-third diatoms, one-fourth fungi, one-fifth unknown, one-fourteenth vascular plant material, and small amounts of arthropod parts and foraminifera (Shanholtzer 1973). The unknown particles may have been inorganic material which is ingested along with organics in *U. pugnax* (Miller 1961). In contrast, I have found *U. pugnax* with stomachs and feces practically filled with vascular plant detritus, presumably that of *S. alterniflora*. Schwartz and Safir (1915) found mostly algae and other vegetable matter along with inorganic particles in the guts of *U. pugnax* and *U. pugilator*. They state that fiddler crabs readily consume decaying animal tissue. This is apparently also true of *U. minax*, which has been observed feeding on algae, organic debris and dead fish (Gray 1942). *U. minax* is believed to use organic detritus as an energy source (Teal 1958, Whiting and Moshiri 1974).

In much of the salt marsh, available foods arise from two major types of primary producer: vascular plants, mostly *Spartina*, and intertidal benthic algae, mostly migratory pinnate diatoms (Pomeroy 1159). Vascular plants account for ⅔ to ¾ of the annual primary production in the salt marsh, with algae being the remainder (Teal 1962, Keefe 1972). Algal production is greatest on the creek-banks and decreases both inland from the levee top and in shaded areas (Pomeroy 1959). Algae are consumed directly by fiddler crabs (Shanholtzer 1973).

Vascular plant carbon is made available to fiddler crabs through its seasonal death and subsequent breakdown into detrital particles (Teal and Teal 1969; Reimold, Gallagher, Linthurst and Pfeiffer 1975). A variety of microflora and microfauna living on these detrital particles are suitable food for fiddler crabs (Darnell 1967).

Teal (1962) described temperate *Uca* as detritus-algae feeders. Because *U. pugnax* absorbed radioactive phosphorous sprayed on marsh substrate, Marples

(1966) concluded that these fiddler crabs were part of the detritus food chain. No definitive statement, however, has been made concerning the relative use of each of these foods. The evidence to date for the use of algae and detritus by temperate western Atlantic *Uca* is presented below.

Crane (1975) states that, while fiddler crabs are known to ingest diatoms, they are usually egested. I, in fact, have photographed living diatoms in *U. pugnax* feces. Shanholtzer (1973), however, demonstrated that *U. pugnax* can assimilate ^{32}P from labeled diatoms offered in high concentrations. I have found *U. pugnax* to readily assimilate carbon originating from natural concentrations of ^{14}C labeled diatoms in marsh mud. Assimilation of diatom carbon was easily detectable after only one hour of feeding. Williams (1962) found higher standing stocks of benthic marsh ditatoms in winter; he attributed the increase in part to the absence of fiddler crab grazing pressure. Evidently, algae are an important food in areas where they are productive.

The diet of temperate *Uca* may contain greater amounts of the detritus-microbe complex where abundant. Perhaps little of this settles on the creekbanks, but tall *Spartina* areas contribute detritus at the rate of about 200 $g \cdot m^{-2} \cdot month^{-1}$, and short grass areas contribute about 115 $g \cdot m^{-2} \cdot month^{-1}$ (Reimold *et al.* 1975). Where *Spartina* is abundant, fiddler crab pellets may be packed with vascular plant detritus.

The detritus-microbe complex is widely believed to provide a suitable energy source for detritivores such as temperate *Uca* (Darnell 1967). Because of the rapid turnover of gut contents, *Spartina* is probably not used directly, even though cellulase has been found in the gut (Kristensen 1972, Shanholtzer 1973). *Spartina* is not readily digested by many detritivores (Pomeroy, Bancroft, Breed, Christian, Frankenberg, Hall, Maurer, Wiebe, Wiegert and Wetzel 1977; Johannes and Satomi 1967; Wetzel 1975, 1977). This may be the case for C4 plants in general (Caswell, Reed, Stephenson and Werner 1973, Caswell and Reed 1975, 1976).

Perhaps a more important attribute of this detritus is to provide a substrate for assimilable decomposer microbes (Pomeroy *et al.* 1977). *S. alterniflora* particles in seawater provide an excellent growth medium for bacteria and the resulting detritus-microbe complex is more nutritive than *Spartina* detritus alone (Burkholder 1956, Burkholder and Burkholder 1956, Burkholder and Bornside 1957). Bacteria are readily ingested by fiddler crabs (Teal 1958, Shanholtzer 1973). Some intertidal macroheterotrophs remove only the microbes from the detritus and egest the substrate (Newell 1965, Darnell 1967).

The nutritive value of *Spartina* may be enhanced by the addition of nitrogen. Its C:N ratio is high (Keefe 1972) as is common for C4 plants (Caswell *et al.* 1973, Caswell and Reed 1975, 1976). The C:N ratio of decomposing *Spartina* increases in the field, presumably because of microbial enrichment (Odum and de la Cruz 1967). Nitrogen can also be adsorbed onto particles from the nitrogen rich surface sediments (Haines, Chalmers, Hanson and Sherr 1977; Krey 1961).

Fungi are important in the breakdown of *Spartina* detritus (Gessner and Goos 1973, May 1974), and have also been found in the gut of temperate *Uca* (Shanholtzer 1973, Pitts and Cowley 1974). In fact, several of the species of fungi that

decompose *S. alterniflora* (Gessner and Goos 1973) have also been found in the midgut of *U. pugilator* (Pitts and Cowley 1974). Yeasts alone, however, cannot satisfy the nutritional requirements of *U. pugilator* (Chrzanowski and Cowley 1977).

Evidently the *Spartina* detritus-microbe complex is a suitable food for the temperate western Atlantic species of fiddler crabs. Haines (1976a, 1976b) and Haines and Montague (1979) show that the stable isotope content ($\delta^{13}C$) of fiddler crab carbon nearly reflects that of *S. alterniflora* in Georgia salt marshes. The differences observed could be explained by the assimilation of a diet partly consisting of carbon derived from benthic algae.

Uca may supplement their protein intake by ingesting bits of carrion, arthropods and nematodes. Collegenase, which has been isolated from the gut of *U. pugilator* (Eisen and Jeffrey 1969, Eisen *et al.* 1973), provides a mechanism for protein breakdown. Particles high in protein may be important to the fiddler crab's nutrition, but their consumption is not believed to represent a major pathway of energy flow.

Finally, fiddler crabs are somewhat selective in their feeding behavior, discriminating between organic and inorganic matter, and ingesting the former (Miller 1961; Altevogt 1955, 1956). Schwartz and Safir (1915) believed fiddler crabs to have a feeding preference for mud high in algal biomass. Consistent differences between substrate $\delta^{13}C$ values, associated plant $\delta^{13}C$ values, and the δ^{13} C values of associated fiddler crabs (Haines 1976b, Haines and Montague 1979) might be explained by preferential feeding. Inclusion in the analysis of sediment particulates not usually available to fiddler crabs, and other methodological problems may also contribute to the consistent differences.

Feeding Periods

In general, fiddler crabs feed whenever they are active on the surface, but feeding intensity varies inversely with concomitant social activity. For the hour or so before and after the tide covers the burrows, intense feeding occurs (Crane 1975, p. 504). Fiddler crabs are inactive at the surface from high tide until their burrows are uncovered; however, the low intertidal marsh species, *U. pugnax* (and to a lesser degree *U. minax* and *U. pugilator*), have frequently been observed to continue feeding for several hours after being covered by incoming tides (Teal 1958, Barnwell 1968, Valiela *et al.* 1974, personal observations, J. R. Robertson pers. comm.). Valiela *et al.* (1974) noticed that all crabs feeding under these conditions were male.

Valiela *et al.* (1974) suggest males compensate for having only one feeding chela (as opposed to two in females) by feeding twice as long as females. However, none of their experiments, which were all performed in the laboratory, were conclusive. In addition, between males and females they detected no differences in nutritional demands, feeding ability, or digestive efficiency. Some difference between males and females seems likely. This interesting suggestion of Valiela *et al.* needs further investigation.

Temperate western Atlantic fiddler crabs are not active on the surface when it is too cold, too hot or too dry, but rains at low tide will stimulate activity (Crane 1975, pp. 442–443). These fiddler crabs are surficially active when temperatures are between about 10°C and 40°C, with greatest intensity between 20°C and 35°C (Teal 1958, 1959; Teal and Teal 1969; Vernberg 1959a; Crane 1943, 1975, pp. 441–444, Miller and Vernberg 1968, Smith and Miller 1973, Gray 1942). *U. pugnax* and *U. pugilator* are active at lower temperatures than *U. minax* (Teal and Teal 1969) possibly because *U. minax* fails to acclimate (Teal 1959).

Nocturnal activity is known for all three species (Salmon 1965), though published descriptions have focused on courtship activity rather than feeding. *U. pugilator* is quite active on the marsh at night (Barnwell 1968) and is reported to feed in droves, make acoustical signals, and copulate on the surface, as long as temperatures are above 18°C (Burkenroad 1947, Salmon 1965, Salmon and Atsaides 1968, Knopf 1966). *U. pugnax* reportedly feeds primarily at low tide during daylight (Valiela *et al.* 1974).

Because *U. pugilator* lives high in the intertidal zone, or on exposed sand beaches, high temperature and desiccation may at times prevent it from feeding sufficiently by day (Teal 1958). On the other hand, high marsh zones are not covered by tides as often as the lower zones are, so, in general, *U. pugilator* has more feeding time each day than have the lower zone species.

The daily and tidal rhythms mentioned in the adaptation section are of unknown importance in the field. They may serve to increase activity at low tides that occur in the mornings and just after dusk (Brown *et al.* 1954; Bennett *et al.* 1957; Barnwell 1966, 1968). The influence of the daily cycle should be relatively more important than the tidal cycle in the higher marsh zones (Barnwell 1968). The effect such rhythms have on feeding activity is also unknown.

As pointed out by Barnwell (1966) individual activity may vary with the stage of molt cycle, reproductive state, and phase of social activity (see Crane 1975, pp. 505–506). Because each of these factors is probably synchronized in a population, their effect to the marsh ecosystem as a whole may be considerable (e.g. Christy 1978, Wheeler 1978).

Effects of Feeding by Fiddler Crabs on the Marsh

Grazing by fiddler crabs may maintain algae in a log phase of growth, with high turnover rates and low standing stock. Ingestion of detritus may affect associated microbes in the same manner. Pace (1977), however, was unable to demonstrate positive effects of grazing by the mud snail *Nassarius obsoletus* on the growth of either benthic algae or the total microbial community found on tidal creekbanks in Georgia.

Ingestion rates of marsh mud have not been determined in the field for temperate western Atlantic fiddler crabs, but one lab study indicates a rate for large *U. pugnax* of about 0.4 g (DW) in a six hour feeding period (Valiela *et al.* 1974). Marsh mud has been said to have about 190 cal · g (DW)$^{-1}$ of organic material, but details about the sample collection and preparation of the mud were not included

(Shanholtzer 1973). Adequate measurements of ingestion rates of algae and detritus by these fiddler crabs have not been made.

Mastication of particulate organic matter by the gastric mill of fiddler crabs should lead to more rapid decomposition of egested detritus. The resulting particle breakdown provides more surface area for microbes (Gosselink and Kirby 1974). In turn, this provides new microbial biomass for fiddler crabs when pellets are re-ingested. Furthermore, this packaging and conditioning of organic matter helps prevent organic accumulation that could cause the marsh surface to go anaerobic.

Bioturbation caused by the feeding activities of fiddler crabs (including sediment scraping and pellet formation) is extensive, and results in a complete turnover and aeration of the top five millimeters or so of marsh surface at least once per year (Kraeuter 1976, Edwards and Frey 1977). Evidence of such reworking is visible after every low tide. Mechanical disturbance of the marsh surface not only should stimulate aerobic decomposition (Hargrave 1976), but also may maintain an environment critical to some of the aerobic bacteria on the marsh surface that are rather specialized because of close proximity to an anaerobic interface (Pomeroy *et al.* 1977).

Mechanical disturbance of the marsh surface may also stimulate algal growth. Disturbance could provide i) more surface area for cells to compete for light, ii) increased availability of nutrients from increased microbial activity, iii) a more favorable aerobic microenvironment, and iv) better proximity to available nitrogen (W. M. Darley pers. comm.). The latter point is arguable since there is more ammonia in the top 5.0 cm of marsh surface than in the overlying water (Haines *et al.* 1977 and personal communications). However, only the surface film of a few millimeters is probably the zone of active nitrogen uptake by algae. Here nitrogen could be quite limiting. If labile nitrogen cannot become available faster than it is absorbed by algae, then it will very likely limit their growth. If algal growth is stimulated, more food will be available to fiddler crabs.

Fecal pellets are produced in great number by fiddler crabs of temperate marshes. A large *U. pugnax* ($\geq$ 1.0 cm carapace width) deposits 0.08 g (DW) $\cdot$ crab^{-1} $\cdot$ day^{-1} of feces and a large *U. pugilator* 0.10 g (DW) $\cdot$ crab^{-1} $\cdot$ day^{-1} (Kraeuter 1976). This represents 100 to 200 pellets per crab per day. Considering the population estimates given earlier, there should be a large number of pellets on the marsh, not all of which may be deposited on the surface however.

The fecal pellets contain coarse detritus (Kraeuter and Haven 1970). Estimates of their total organic content range from 30% (Valiela *et al.* 1974) to 70% (Kraeuter 1976) by weight. Along with other nutrients, the nitrogen content of the feces of *Uca* and of other marsh invertebrates was measured by Kraeuter (1976). *U. pugnax* contributes 9000 μg $\cdot$ m^{-2} $\cdot$ day^{-1} of Kjeldahl nitrogen, more than any of the other benthic invertebrates tested, including *Littorina irrorata.* The effect these pellets have on microbial processes such as detrital decomposition or algal production is unknown, but mechanisms for possible enhancement of such processes are conceivable (Hargrave 1976, Kitchell, O'Neill, Webb, Gallepp, Bartell, Koonce and Ausmus 1979).

SUMMARY AND CONCLUSIONS

According to Powers (1977) biological information available on *Uca* is unsurpassed among crab genera. Crane (1975) reviewed most of the behavioral and morphological literature, Powers (1977) provides an extensive bibliography of research on fifteen *Uca* species, and this review compiles much of the physiological and ecological work on the three temperate western Atlantic species. The wealth of information has allowed a detailed understanding of major features of the life histories of these three species. Recent studies of larval release by Wheeler (1978) and Christy (1978) help to complete the picture. Still unknown, however, are the number of clutches per female per year, actual sex ratios, and the stimuli responsible for larval settlement. The question of sex ratio can be quickly answered with a specifically designed sampling program.

The relative importance of predation, competition, food supply and habitat in controlling the densities of temperate western Atlantic fiddler crabs is an open area for research. The few published approaches to this problem provide background for more definitive future studies.

The studies of Shanholtzer (1973), Wolf *et al.* (1975), and Krebs and Valiela (in prep.) provide details of *U. pugnax* population ecology and energetics. Direct measurements are lacking for the ingestion and assimilation of various foods. The methods Wetzel (1975, 1977) used on snails may be modified for *Uca*.

The population ecology and energetics of *U. pugilator* is less well known than that of *U. pugnax; U. pugilator*, however, has been used in many of the laboratory studies of fiddler crab physiology. In contrast, ecologists and physiologists have nearly ignored *U. minax*, which occurs in great number along the fresher more inland waters.

Temperate western Atlantic fiddler crabs apparently feed on whatever nutritious carbon sources are available. Selection of foods is primarily by size and organic or amino acid content. Available foods vary with location: creekbank carbon is primarily of diatom origin, but surface sediments of the back levee meadow marsh contain decaying *Spartina* detritus with some algae. *Spartina* detritus is made nutritious by decomposers such as bacteria and fungi and perhaps by adsorbed nitrogen. The algae-detritus diet is supplemented by small amounts of high protein carrion, arthropods and perhaps nematodes. Feeding studies using stable and radioactive carbon isotopes should reveal the proportions of the fiddler crab diet originating from algae and from vascular plants (e.g., Haines 1976a, 1976b; Haines and Montague 1979; Wetzel 1975, 1977).

Temperate western Atlantic fiddler crabs face a complex optimization problem whereby fitness is maximized within the rigorous and variable constraints of both the intertidal salt marsh environment and the evolutionary history of the crabs themselves. Specialized physiological, morphological and behavioral adaptations help account for their success in temperate salt marshes. Adjustments for changes in salinity and temperature are accomplished as long as a supply of water is nearby. Burrows contain necessary water, offer protection from weather and predators, and furnish privacy for molting, incubation of eggs, and probably copulation.

The significance of endogenous rhythms to field populations of *Uca* needs to be clarified. These rhythms probably affect feeding activity and respiration rates in the field and should be considered in the design of field and laboratory studies. Explaining their significance should contribute to a general understanding of adaptation of intertidal life.

The effect of the environment on fiddler crabs has received far more attention than have the effects of fiddler crabs on their environment. Temperate western Atlantic *Uca* not only graze algae, microbes and meiofauna, but also may enhance the growth of *Spartina alterniflora*, microbial decomposers, and benthic algae. The grazing pressure exerted by fiddler crabs varies with species, location, tidal regime, temperature, and food availability. Total grazing pressure is greatest when low tides occur in both morning and evening during the milder summer months. In Georgia, winter grazing occurs on warm days, but is generally minimal. The significance of night grazing is unknown, but, except perhaps for *U. pugilator*, night grazing in temperate *Uca* is probably considerably less common than grazing by day.

Burrow excavation, feeding bioturbation, and fecal pellets are activities and byproducts of temperate western Atlantic *Uca* that may increase carbon and nutrient flow in salt marshes. Mechanisms for such enhancement have been suggested throughout this review, but have never been addressed experimentally. Manipulation of fiddler crab densities and the density of their byproducts or simulated byproducts (e.g., burrows, feeding marks) should help establish the total impact of these crabs on the salt marsh ecosystem. After such manipulation, measures of benthic photosynthesis, meiofaunal densities, ATP, chlorophyll, respiration, nutrient flow, etc. can establish the net effect of the fiddler crab treatments. The potential exists for fiddler crabs to affect the salt marsh in a manner which insures its own food resources, as illustrated in the summary diagram (Figure 1). In the diagram, algae and aerobic decomposer microbes are examples of fiddler crab foods. Feeding by the crabs can relieve or prevent overcrowded conditions among the food organisms. Both burrowing and feeding aerate and mix soils and thereby increase nutrient and oxygen availability for better future growth of algae and decomposers. Burrows may also improve cordgrass growth. Both algae and decomposers should benefit from fecal pellets which contain nutrients and conditioned, ground and concentrated organic matter.

The fiddler crab should be considered a whole system of influences that interacts both positively and negatively with its environment. It not only responds to its surroundings, but also creates its surroundings to some degree. Being, in this way, an integral part of an ecosystem should have survival value for fiddler crabs that inhabit salt marshes. Perhaps all organisms benefit from similar interactions while contributing to the structure and function of an ecosystem (for related discussion, see Owen and Wiegert 1976, Mattson and Addy 1975, Chew 1974).

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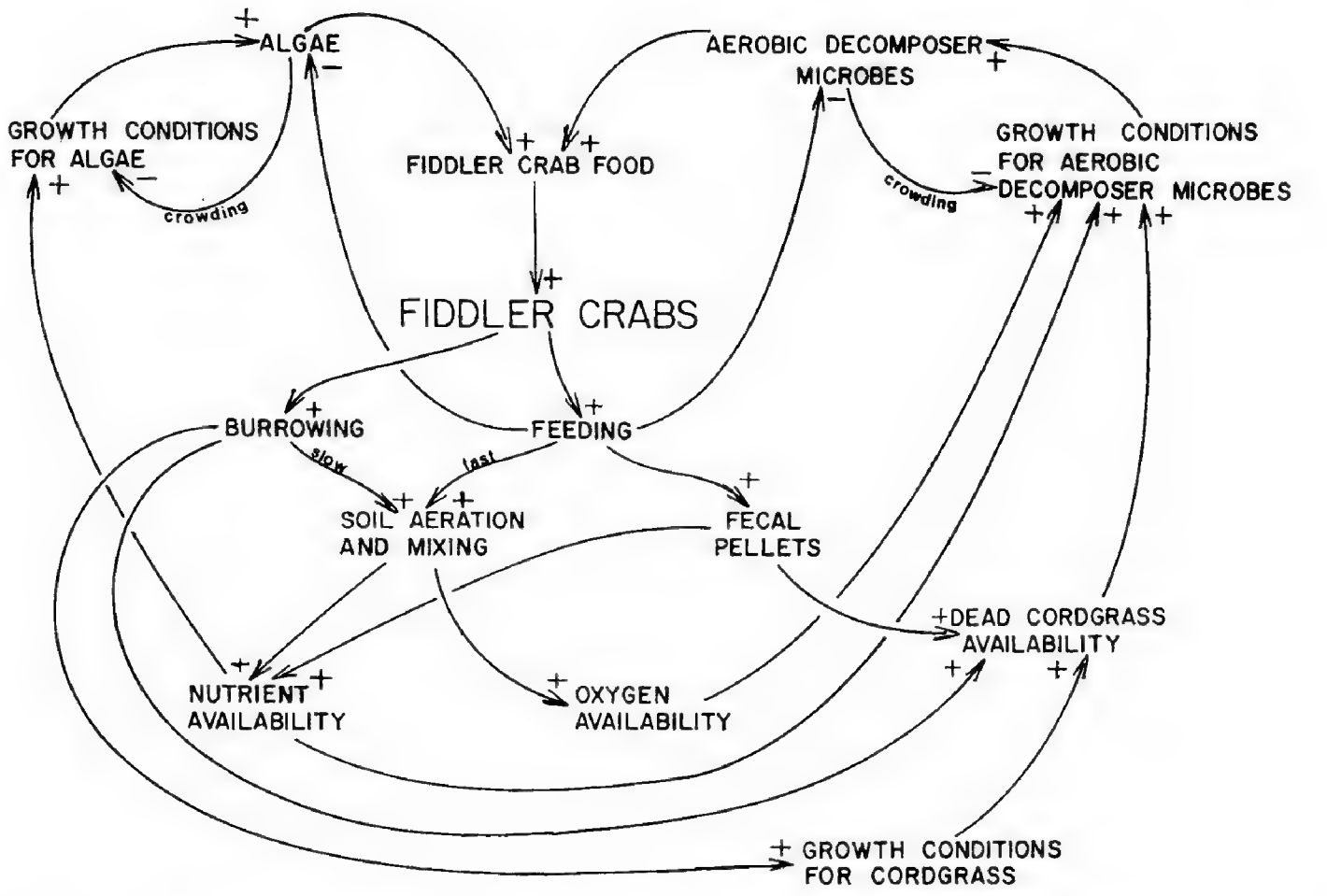

FIG. 1. Fiddler crabs potentially affect the salt marsh in a manner which improves the production of its foods. Key to diagram: FIDDLER CRABS → + FEEDING, FEEDING → - ALGAE; FIDDLER CRABS positively influence FEEDING (i.e., more fiddler crabs mean more feeding and less fiddler crabs mean less feeding); FEEDING negatively influences ALGAE (i.e., more feeding means less algae and less feeding means more algae).

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THE GENUS *PHOTIS* (CRUSTACEA: AMPHIPODA) FROM THE TEXAS COAST WITH THE DESCRIPTION OF A NEW SPECIES, *PHOTIS MELANICUS*

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ABSTRACT

Members of the amphipod genus *Photis* occurring along the Texas coast are reviewed and a key for their identification is presented. One new species, *Photis melanicus*, is described. It is distinguished by its unusual body pigmentation, lack of stridulating structures in the male and bifid accessory claws on posterior peraeopod dactyls.

INTRODUCTION

The genus *Photis* is composed of a large number of species found throughout the world (Barnard 1962, 1973). Until recently only *Photis pugnator* Shoemaker 1945, was reported from the Gulf of Mexico. McKinney *et al.* (1978) described a new species, *Photis macromanus*, which is commonly found in offshore waters of the western Gulf of Mexico. A third species, *Photis melanicus*, is described as new in this paper. This rare species is apparently similar both morphologically and ecologically to as yet undescribed photids from the west coast of North America.

ILLUSTRATIONS

Figure follows the format established by J. L. Barnard (1970). Capital letters designate specific structures. Lower case letters preceding the capital letter designates a specific individual. Lower case letters or numbers following the capital letter modify the description of the structure: B = labrum (upper lip); C = coxa; D = dactyl; G = labium (lower lip); M = mandible; N = gnathopod; Q = mandibular molar; S = maxilliped; T = telson; U = uropod; X = maxilla; l = left; w = palm; x = medial.

TAXONOMY

The genus *Photis* was placed in the superfamily Corophioidea by J. L. Barnard (1973).

Photis Kroyer, 1842

Diagnosis. Article 3 of antenna 1 as long as article 1; accessory flagellum absent or vestigal; uropod 3 with elongate peduncle, outer ramus as long as peduncle, inner ramus half or less the length of peduncle; mandibular palp article 3 clavate.

Key to the species of *Photis* from the Texas coast

1a. Article 2 of gnathopod 2 and/or distal edge of coxa 3 without stridulating ridges.
Posterior pereopod dactyls with bifid accessory claws ..... *Photis melanicus*, n. sp.
1b. Article 2 of gnathopod 2 and/or distal edge of coxa 3 with stidulating ridges.
Bifid accessory claws absent 2
2a. Dactyl of adult male greatly overlapping the V-shaped palm,
palm lacking process on inner margin.
Dactyl of female simple ..... *Photis macromanus*, McKinney *et al.* (1978)
2b. Dactyl of adult with a process on inner margin, palm with a long
tooth defining a deeply excavate sinus. Dactyl of female with
teeth on inner margin ..... *P. pugnator*, Shoemaker (1945)

Photis pugnator Shoemaker, 1945

Diagnosis. Male: posterodistal edge of coxa 3 and article 2 of gnathopod 2 with stridulating ridges (male); dactyl of gnathopod 2 (male) with a medial process on inner margin; shorter than palm, palm with a deep excavation and long defining tooth. Female: Like male but lacking stridulating ridges, Palm of gnathopod 2 slightly oblique, sinus shallow. Dactyl with 2 teeth on inner margin.

Material. Specimens from 7.5 fm. reef, 26°50′N 95°40′W. This species is apparently restricted to such hard bottomed areas. 7.5 fm. reef is a serpulid type reef which rises above the surrounding clay and sand bottoms.

Photis macromanus McKinney, Kalke and Holland, 1978

Diagnosis. Male. posterodistal edge of coxa 3 and article 2 of gnathopod 2 with stridulating ridges; dactyl gnathopod 2 greatly overlapping the deeply incised palm. Female: Palm of gnathopod 1 lacking a defining tooth; palmar sinus shallow to absent. Dactyl normal, lacking posterior teeth.

Material. Specimens from 18 to 42 m depth along the Texas coast. This is a common and widespread species on the coastal bottoms of the area.

Remarks. Although common throughout the year, this species is seasonally most numerous from March to June. Ovigerous females are prevalent in March and April.

Distribution. Gulf of Mexico, Texas coast.

Photis melanicus, new species

Description. Male 1.40 mm. Head normal for genus, eyes with widely spaced ommatidia and black central area. Antenna 1: Articles 1 and 2 subequal, third article 0.9 times as long as preceding ones; flagellum with 5 articles, each with 1–2 elongate setae; articles of the peduncle and some flagellar articles with spots of black pigment which persist in preservation. Antenna 2: Article 3 of peduncle slightly inflated, article 4 slightly shorter than 5; flagellum with 3 subequal articles; some articles of antenna with pigment spots as in antenna 1. Upper lip: bilobed. Mandible: Molar process produced, toothed on outer margins with short plumose accessory setae, molar scale on right, setose area on left; 3 accessory blades on right and 4 on left, lacinia mobilis on both; incisor produced and toothed; palp with 3 articles of length ratios—24: 60:49, article 2 with ventral setae, article

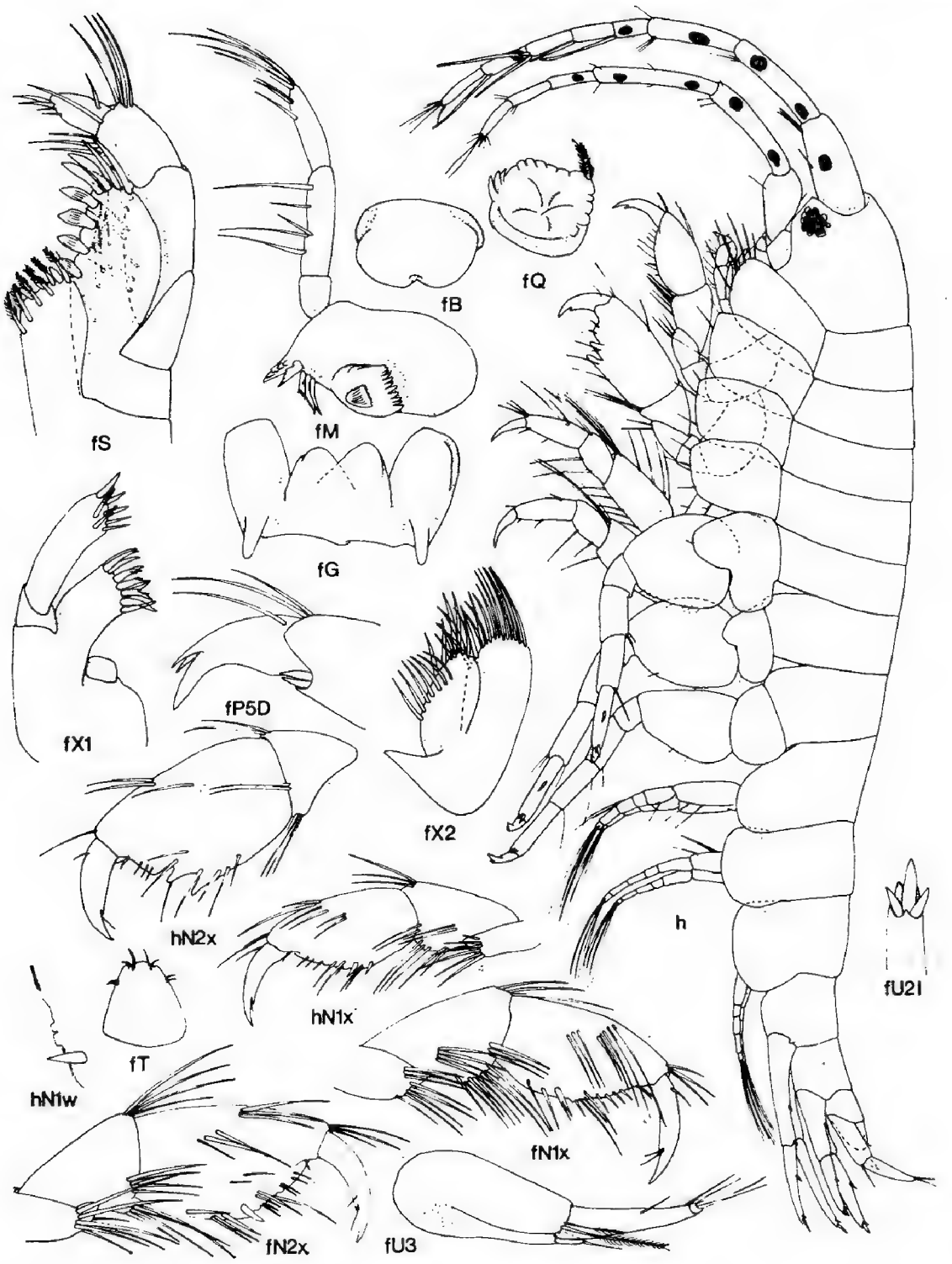

FIG. 1. *Photis melanicus*, new species, h = male, 1.40 mm; f = female, 2.26 mm.

3 with terminal setae. Lower lip: prominent inner lobes; outer lobes widely spaced, distal ends quadrate. Maxilla 1: Inner plate unarmed, quadrate; outer plate with 9 spine teeth; palp biarticulate, distal article 2.9 times as long as the first, palp with 5 terminal and 2 subterminal oblique setae. Maxilla 2: Inner plate with terminal setae and oblique row of facial setae along medial edge. Maxilliped: Inner plate quadrate with 3 terminal chisel teeth and oblique row of 6 subterminal, plumose setae; outer plate with 3 large chisel teeth on medial edge and 4 stout terminal spines; palp with 4 articles, article 2 medially setose, articles 3 and 4 terminally setose, article 4 with 1 laterobasal seta. Gnathopod 1: Coxa subquadrate with long distal setae; article 2 somewhat inflated; article 3 with posterodistal setae; article 4 with three anterodistal setae and 5 posteromedial setae; arti-

cle 6 with 2 medial and anterodistal setae, palm oblique, lower edge somewhat rugose, corner, defined by 2 spines; dactyl closing on defining spines. Gnathopod 2: Larger than gnathopod 1; coxa subquadrate, distal edge with fewer setae than coxa 1; article 2 inflated, stout; articles 3 or 4 with posterodistal setae; palm slightly oblique with 2 deep sinuses, the lower sinus bordered by tooth which defines the palm; palm and posterodistal edge of article 6 with stout setae; dactyl stout, closing on defining tooth. Pereopod 3: Coxa subquadrate, anterior and posterior margins of articles setose, anterodistal edge of article 4 with elongate setae. Pereopod 4: Like pereopod 3. Pereopod 5: Coxa with posterior lobe; article 2 inflated, posterior margin lined with setae; remaining articles poorly setose; posterior margin of article 6 with single medial spine and 2 distal locking spines; dactyl with bifid accessory claw. Pereopod 6: Coxa shorter than preceding ones, bifid; otherwise like pereopod 5. Pereopod 7: Coxa rounded, wider than long; article 2 with posterior margin expanded; remaining articles poorly setose; dactyl with bifid accessory claw. Epimeral plates: Rounded, unarmed. Uropod 1: Outer margin of peduncle with 2–3 spines, inner margin with 1 distal spine; inner ramus with 1–2 marginal spines and a terminal nail; outer ramus with 2–3 marginal spines and a terminal nail. Uropod 2: Inner margin of peduncle bare, outer with 2 spines; rami with 2 marginal spines and a terminal nail each. Uropod 3: Peduncle with plumose distal setae; inner ramus short and scale-like with terminal setae; outer ramus with minute second article, distal article with 2 elongate setae. Telson: Entire, inflated, with 2 distal spines paired with lateral accessory setule, lateral margins of telson with pair of setules. Gills: Present on pereopods 2–6.

Description of female. 2.26 mm. Gnathopod 2 like 1 but slightly larger, palm shorter than in gnathopod 1 and defined by a single spine rather than 2. Articles 4, 5 and 6 of gnathopods with more medial facial setae than in the male, palms are similar in both. Uropods generally more setose than in male.

Types. Holotype, USNM 172292, male 1.4 mm. Allotype, USNM 172293, female 2.26 mm. with a Paratype series of 3 males, USNM 173394.

Type-locality. Types taken from stations NT:NMFS 108A-C located within the area 28′N to 28°30′N and 95°00′W to 95°30′W.

Material examined. Specimens from the type-locality.

Distribution. Known only from type-locality (Texas coast).

Remarks. Although the male described was small by comparison to the female allotype other larger males were examined. All were similar in lacking the stridulating ridges as well as other diagnostic characteristics. The smaller male was illustrated because of its unusually well preserved condition compared to other material on hand.

Relationships. The relationships of this species are not clear. The uniquely bifid accessory claw on pereopods 5–7, lack of stridulating ridges and double palmar sinus on gnathopod 2 separates it from all other members of the genus. This species does apparently share some common characteristics with as yet undescribed (and unseen) material from California, most significantly the lack of stridulating ridges and general size (G. Gillingham, Moss Landing Marine Lab, personal communication).

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ABUNDANCE, REPRODUCTIVE SEASONALITY AND HABITAT PREFERENCES OF AMPHIPOD CRUSTACEANS IN SEAGRASS MEADOWS OF APALACHEE BAY, FLORIDA[1]

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ABSTRACT

A fifteen-month survey of amphipod fauna in Apalachee Bay, Florida, produced 31 species. The majority of the amphipod species was associated with vegetation (primarily seagrasses) and only *Ampelisca* species were most abundant in unvegetated habitats. An analysis of patterns in abundance and reproductive activity for the 14 numerically dominant species showed that seasonality of abundance was not associated with physical-chemical aspects of the environment or with seasonal patterns in macrophyte biomass. Rather, abundances were most closely related to reproductive processes in individual species and, in certain cases, to abundance of fish predators. Species which appeared to be most heavily influenced by seasonal occurrences of predators corresponded with those epibenthic forms known to be positively selected as prey by pinfish, *Lagodon rhomboides*. It was concluded that mechanisms which regulate amphipod abundances vary with species, season, and locality. The blade density and species composition of seagrass beds may affect amphipod species directly or indirectly or through mediation of the behavior of predators.

INTRODUCTION

Although considerable literature exists concerning the population dynamics of individual amphipod species in marshes (Farrell 1970, Rees 1975, Van Dolah 1978), sandy beaches (Croker 1967; Dexter 1967, 1971; Mills 1967; Sameoto 1969) and mud bottoms (Jones 1948, Feeley 1967, Thoemke 1979), little is known about species associated with seagrass habitats. Some information is available on the biology of amphipods of *Zostera marina* beds (Nagata 1960; Marsh 1973; Nelson 1978, 1979a,b; Caine 1979); however, only two studies including data on amphipods associated with *Thalassia testudinum* are known to this author (Brook 1975, Zimmerman 1978). Nelson *et al.* (in review) provide the only data on amphipods associated with *Halodue wrightii*. This lack of information is surprising given the fact that amphipods are among the most important prey items

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for fishes inhabiting seagrass meadows (Carr and Adams 1973; Brook 1975, 1977; Adams 1976; Stoner 1979a,b; Stoner and Livingston 1980) and that several studies have dealt with the significance of predation on these amphipods (Young *et al.* 1976; Young and Young 1977, 1978; Nelson 1978; Reise 1978). Because no data are available on the biology of seagrass-associated amphipods from the Gulf of Mexico the objectives of the present study were to: 1) describe seasonal patterns in abundance for the most numerous amphipods in Apalachee Bay, Florida, and to discuss these patterns in terms of reproductive seasonality, macrophyte abundance, and fish predation, 2) discuss habitat preferences of the amphipods with particular reference to the composition of macrophytes at collecting sites, and 3) where possible, relate the findings in Apalachee Bay to other geographical areas.

MATERIALS AND METHODS

Four collecting sites were marked in the shallow subtidal regions of Apalachee Bay, Florida, offshore from the Econfina (E10, E12) and Fenholloway (F11, F12) Rivers (Fig. 1). Fenholloway station 11 (unvegetated site) had a low total macrophyte standing crop (annual mean = 9.3 g dry wt/m^2) composed of the tracheophyte *Halophila engelmanni* and lesser amounts of red algae. Fenholloway station 12 (low macrophyte biomass site) had a mean annual macrophyte biomass of 141 g dry wt/m^2, composed primarily of *Syringodium filiforme* and *Thalassia testudinum* in approximately equal amounts, with small amounts of *Halodule wrightii* and various green and red algae. The macrophyte composition at *Econfina* 10 (medium macrophyte biomass

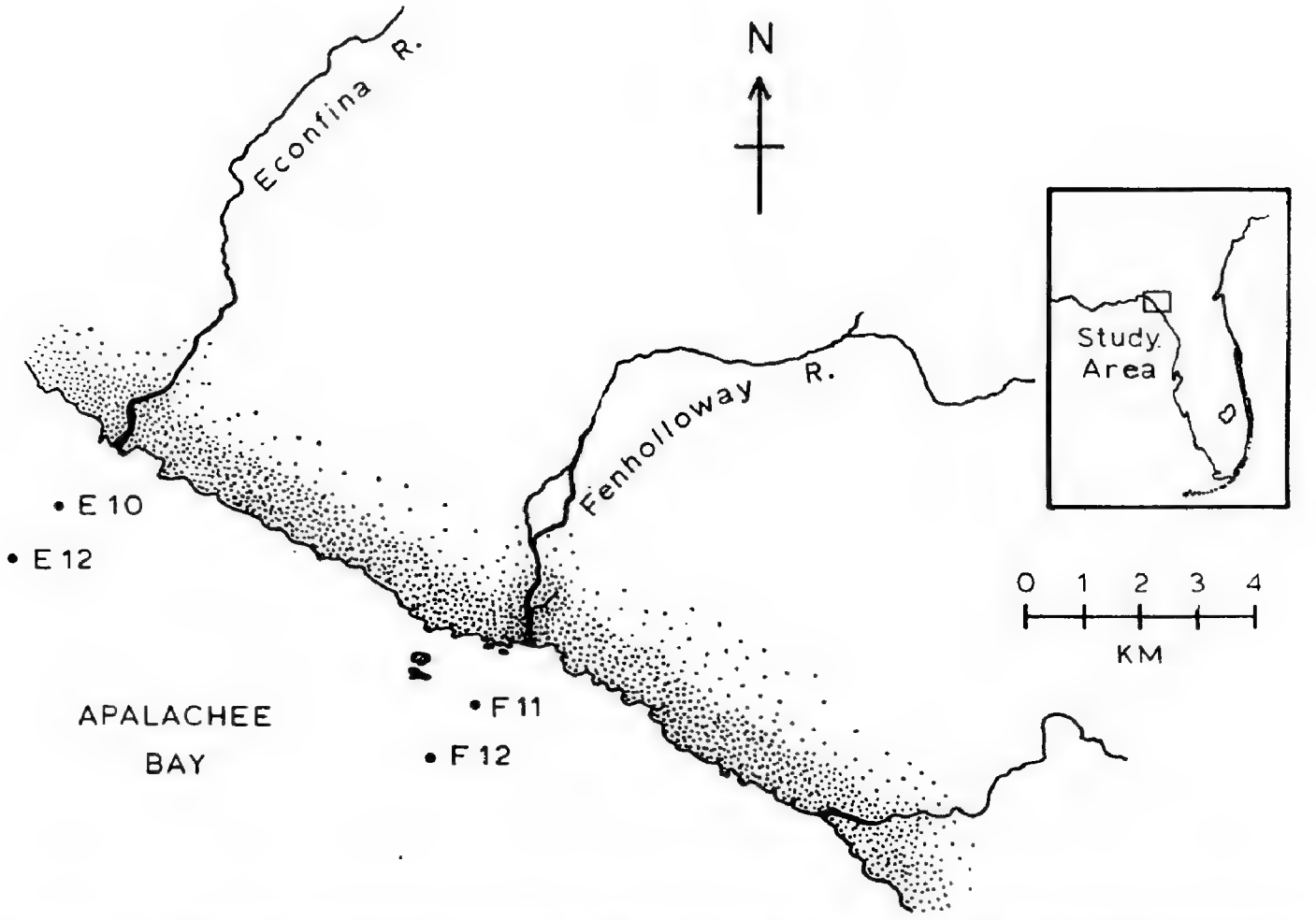

FIG. 1. Locations of collecting sites off the Econfina and Fenholloway drainage systems in Apalachee Bay, Florida.

site) was very similar to that at Fenholloway 12 except that the mean annual standing crop was higher (215 g dry wt/m^2). Econfina 12 was characterized by high mean annual macrophyte biomass (320 g dry wt/m^2). *Thalassia testudinum* made up a larger proportion of the total macrophyte biomass at this station than at the other stations (approx. 70%) and *S. filiforme* was less important. A similar assemblage of red and green algae was found at all three vegetated sites. Macrophyte standing crops were low during winter months and reached maximum values in September (R. J. Livingston, unpublished data). The rationale for station choice was discussed in earlier reports (Stoner 1980a).

Analysis of water quality data taken during the survey indicated that all of the sampling sites were polyhaline with salinities ranging from 17 to 34 ‰ at the outer stations and 17 to 32 ppt at the inner stations. However, mean salinities were not different at the four sites (ANOVA, $P < 0.05$) (Table 1). Turbidities were somewhat higher at the Fenholloway stations, but because of wide variation at individual stations, water color at the four sites did not differ significantly despite mean values ranging from 53.1 to 13.2 Pt-Co units. Mean water depths were slightly different by station but ranged only from 1.6 to 2.0 meters. Secchi disc readings were slightly greater at Econfina 12. Daytime dissolved oxygen (surface and bottom) was never less than 100% of the saturation level at any station. Water temperature was similar at all four stations, ranging from 7.2°C in December, 1976 to 32.2°C in July, 1977. The sediments at the four stations were similar (Stoner 1980a).

The pinfish, *Lagodon rhomboides*, was the most numerous amphipod-consuming fish in Apalachee Bay, representing approximately 70% of the trawlable ichthyofauna (Stoner, in prep. a). Abundance of pinfish was maximum in mid-summer and very low during winter (Fig. 2), as were the values for total number of fishes collected.

TABLE 1

Summary of physical-chemical factors at four stations in Apalachee Bay, Florida, December, 1976 through February, 1978. (mean ± S.D., n = 15). ^{o} and * indicate that mean values were not different (ANOVA and Duncan's multiple range test, $P < 0.05$).

Variable	Fen 11	Fen 12	Econ 10	Econ 12
Salinity (ppt)				
surface	25.6 ± 4.8*	28.2 ± 4.8*	23.0 ± 4.5*	26.6 ± 4.6*
bottom	25.9 ± 5.0*	28.5 ± 4.8*	23.2 ± 4.5*	27.3 ± 3.9*
Salinity Range	17.1 - 31.6	21.0 - 33.9	17.1 - 31.6	17.1 - 33.9
Turbidity (JTU)				
surface	6.8 ± 6.2^{o}	5.7 ± 5.0*^{o}	3.3 ± 1.2*	3.5 ± 1.8*
bottom	7.9 ± 7.8^{o}	6.6 ± 5.5*^{o}	3.6 ± 1.3*	3.5 ± 1.5*
Color (Pt-Co Units)				
surface	52.1 ± 52.0*	44.7 ± 60.5*	48.9 ± 68.1*	17.9 ± 28.4*
bottom	47.0 ± 49.7*	31.1 ± 43.5*	38.7 ± 47.1*	15.2 ± 16.8*
Secchi Reading (m)	1.2 ± 0.5*	1.3 ± 0.5*	1.4 ± 0.5*	1.8 ± 0.4
Depth (m)	1.7 ± 0.4*^{o}	1.7 ± 0.4*^{o}	1.6 ± 0.3^{o}	2.0 ± 0.4*
Dissolved Oxygen	All samples >100% saturation (surface and bottom)			

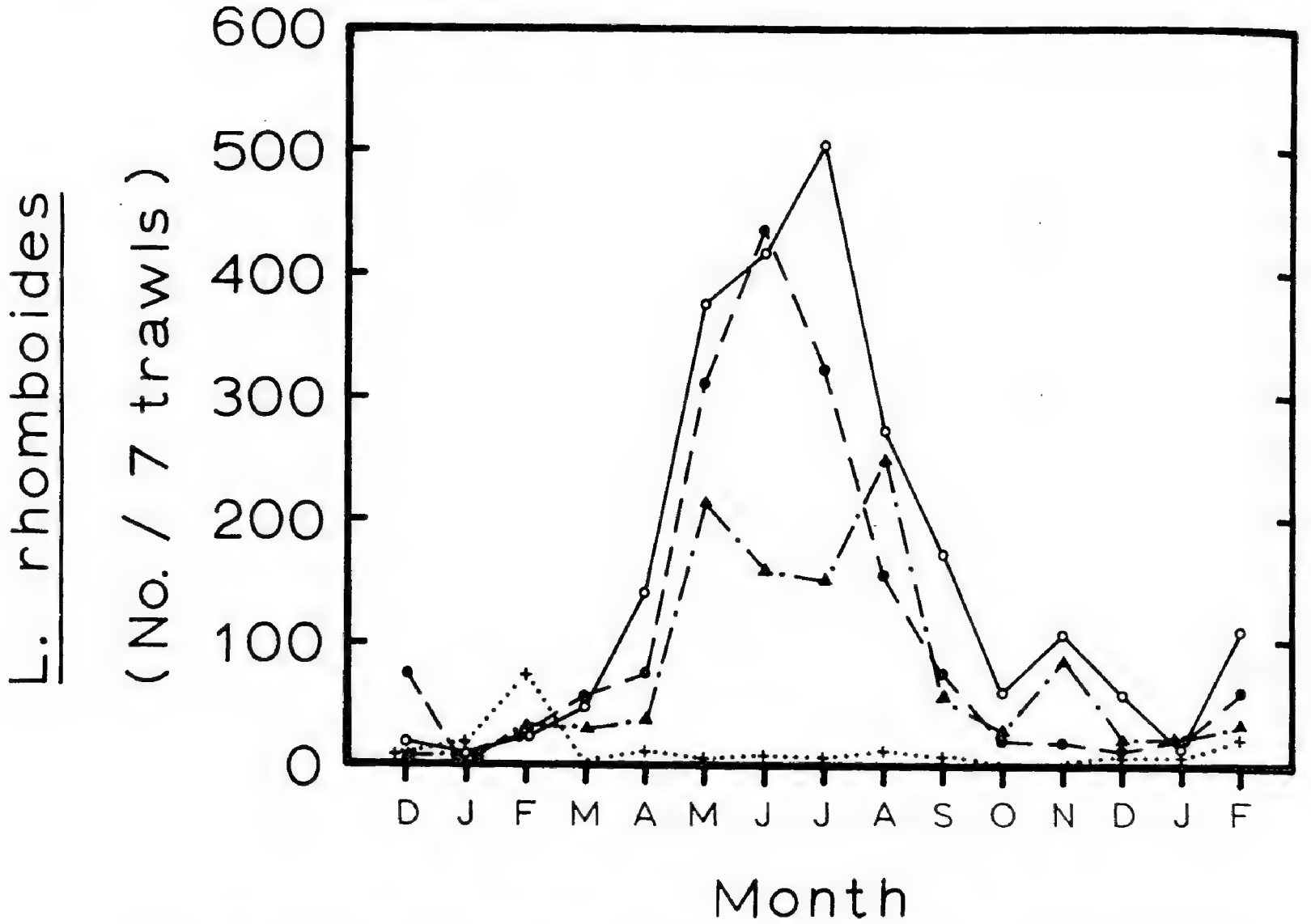

FIG. 2 Number of *Lagodon rhomboides* collected in Apalachee Bay, Florida, from December, 1976 to February, 1978. Crosses = Fenholloway 11, triangles = Fenholloway 12, closed circles = Econfina 10, open circles = Econfina 12.

Amphipods were collected monthly (December, 1976 to February, 1978) with hand-held cores 7.6 cm in diameter (45.32 cm^2). Core depth was 12 cm. On the recommendation of Lewis and Stoner (1980), a 0.5 mm screen was used to retain the animals collected in cores. Recently it was shown that core methods are an appropriate means for collecting amphipods and that concern about undersampling epifaunal forms with core devices is unjustified (Stoner *et al.*, in review). Benthic samples were preserved in a Formalin-seawater mixture and stained with rose bengal. In the laboratory macrofauna were sorted by hand and identified to the lowest possible taxa. The presence of females with eggs in the brood pouch was recorded for all amphipod species. Because some amphipods are known to carry eggs through the winter at higher latitudes, the presence of ovigerous females is not always a valid indicator of reproductive activity. However, because the smallest amphipods occurred during the periods when ovigerous females were present for all of the numerous species in Apalachee Bay, reproductive seasonality derived from data on the presence of ovigerous females was deemed appropriate.

RESULTS

Thirty-one amphipod species were taken in monthly collections at the four sampling sites in Apalachee Bay (Table 2). Seasonal abundances, habitat preferences, and reproductive activities are discussed for each of the abundant species.

TABLE 2

Amphipod species collected at four stations in Apalachee Bay, Florida. Total number of individuals collected in monthly sampling between December, 1976 and February, 1978.

Rank	Species	F11	F12	E10	E12
1	*Elasmopus levis*	9	127	270	150
2	*Lembos* sp. A	4	132	91	311
3	*Rudilemboides naglei*	6	93	106	286
4	*Cymadusa compta*	8	85	195	111
5	*Ampelisca vadorum*	163	45	70	44
6	*Lysianopsis alba*	8	120	119	36
7	*Ampelisca verrilli*	126	11	42	9
8	*Pontogenia* sp. A	7	67	47	56
9	*Synchelidium americanum*	25	70	41	32
10	*Carinobatea carinata*	2	20	24	96
11	*Batea catharinensis*	24	45	22	39
12	*Melita appendiculata*	7	66	16	2
13	*Gitanopsis* sp. A	1	34	34	17
14	*Lysianopsis hirsuta*	0	16	14	36
15	*Paracaprella tenuis*	4	29	12	20
16	*Corophium louisianum*	17	12	13	0
17	*Paraphoxus* sp. A	1	20	18	11
18	*Erichthonius* sp. A	1	12	13	9
19	*Tiron tropakis*	2	29	2	2
20	*Cerapus* sp. A	0	20	8	5
21	*Corophium* sp. A	10	14	1	1
22	*Stenethoe* sp. A	2	7	4	3
23	*Listriella* sp. B	4	2	4	1
24	*Gammarus macromucronatus*	0	1	1	3
25	*Heterophlias seclusus*	0	3	1	0
26	*Colomastix* sp. A	0	0	2	1
27	*Gammarus mucronatus*	0	0	1	1
28	*Leucothoe* sp. A	0	0	2	0
29	*Listriella* sp. A	0	1	0	0
30	*Listriella* sp. C	0	0	0	1
31	*Stenethoe* sp. B	1	0	0	0

Elasmopus levis Smith 1873 (Melitidae) was the most numerous amphipod collected. This species dominated the amphipod fauna at station E10 (medium vegetation) with peak populations (1096/m^2) in May (Fig. 3). *Elasmopus levis* was nearly constant in abundance at 300 individuals/m^2 at the heavily vegetated station (E12), occurred in distinct April and November peaks at F12 (low vegetation), and was rare at unvegetated station F11. The distribution of *E. levis* appeared to be patchy since a large percentage of monthly collection was often taken in two or three core samples. Patchiness in the distribution of the species and resulting sampling problems may explain erratic population densities at E10. Ovigerous animals were collected from May to September (Fig. 4) corresponding with the reproductive season reported by Bousfield (1973). A repro-

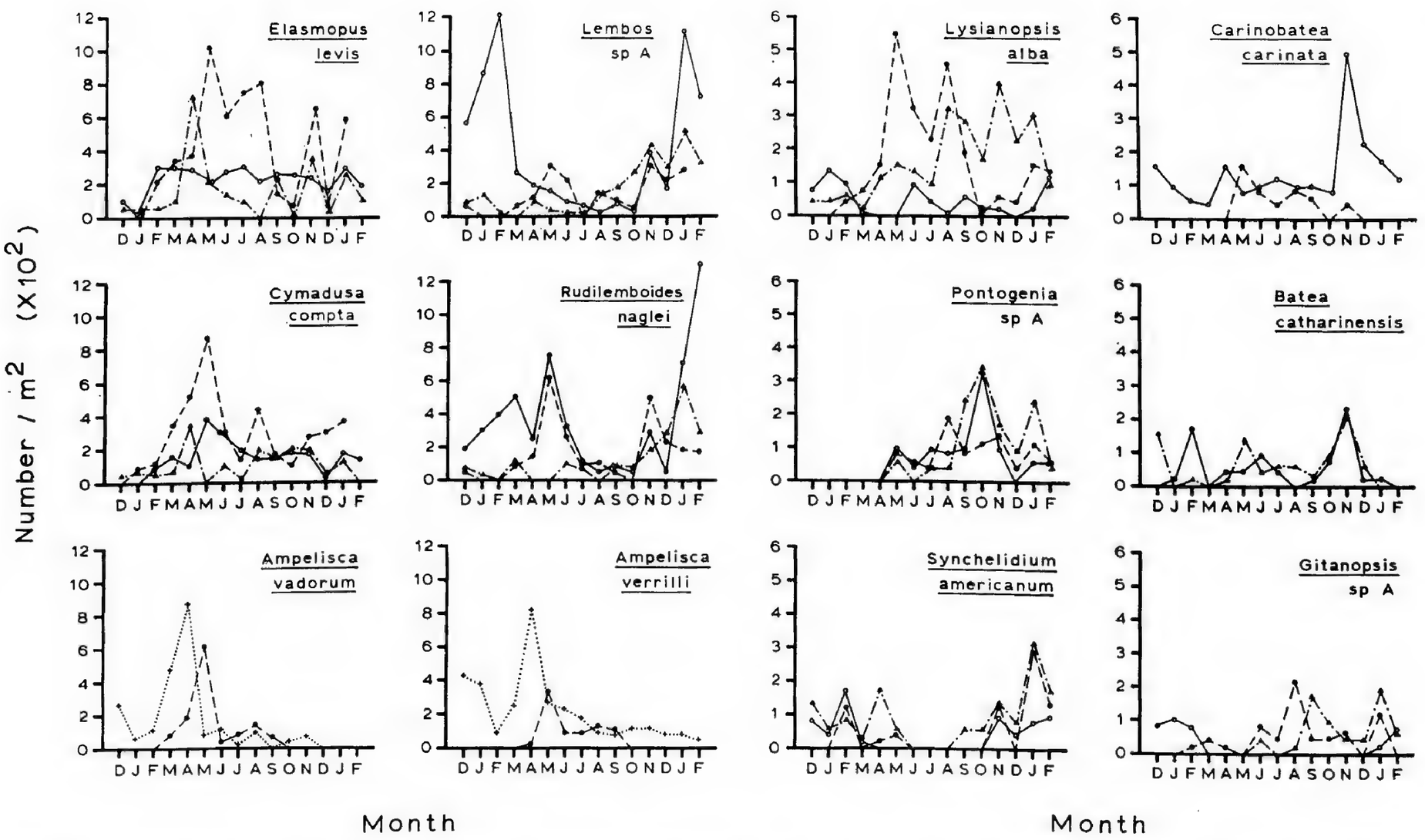

FIG. 3. Abundance of numerically dominant amphipods in Apalachee Bay, Florida, from December, 1976 to February, 1978. Crosses = Fenholloway 11, triangles = Fenholloway 12, closed circles = Econfina 10, open circles = Econfina 12.

ductive season extending from February through December was found for *E. levis* from North Carolina (Nelson 1978). In the spring, *E. levis* populations increased as an apparent reflection to reproductive activity; however, populations at Fenholloway 12 declined after a brief peak in April.

Lembos sp. A (cf. *L. smithi*) (Aoridae) was the dominant amphipod at the most heavily vegetated site (E12), but was also abundant at other vegetated stations (E10, F12). Few *Lembos* were collected at the unvegetated station (F11). Seasonality in abundance, however, varied by station (Fig. 3). Ovigerous from March through December (Fig. 4) *Lembos* populations reflected reproductive activity at E10. At F12, populations were low during the early part of the reproductive period and at the heavily vegetated station (E12), *Lembos* demonstrated a dramatic decline in abundance during the period of increase in fishes on the station in spring. At all three stations, *Lembos* populations increased in the late fall when fishes left the grass flats (see Fig. 2).

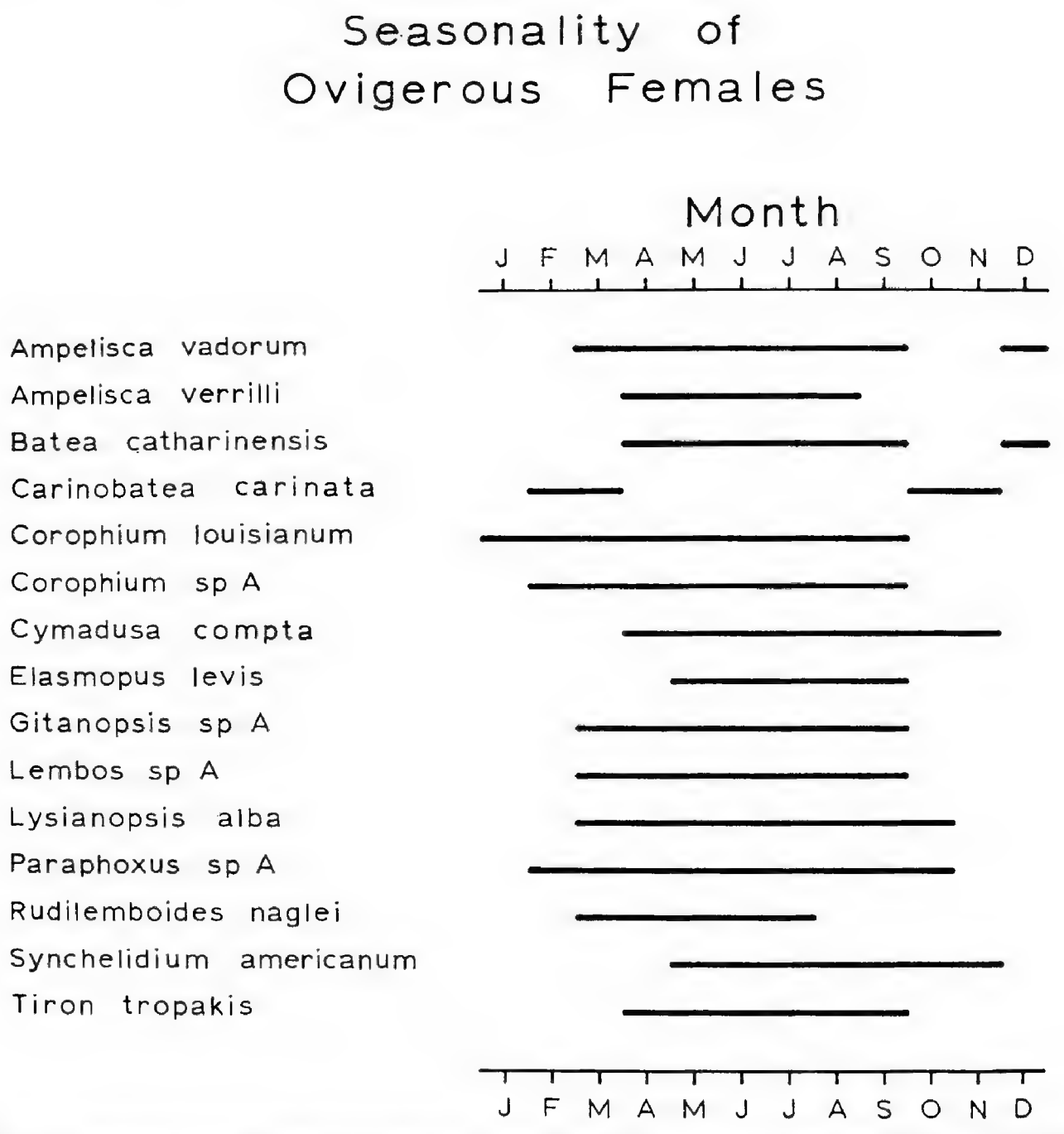

FIG. 4. Seasonality of ovigerous females in amphipods from Apalachee Bay, Florida. (1977 and 1978).

Cymadusa compta Smith 1873 (Ampithoidae), like *E. levis*, was most abundant at station E10 and was rare at the unvegetated site F11. Reproductive season of *C. compta* in Apalachee Bay extended from April to November (Fig. 4). Ovigery was reported to occur from May to November by Bousfield (1973) and from January to November by Nelson (1978). Reproductive seasonality was reflected by animal abundances (Fig. 3) at E10 and E12, but high population densities at F12 occurred only at the beginning of the reproductive season.

Total abundance of *Rudilemboides naglei* Bousfield 1973 (Aoridae) was directly correlated to mean annual standing crop of benthic macrophytes at an individual station ($R = 0.967$, $P < 0.05$); however, seasonal abundances (Fig. 3) were not correlated with seasonalities of macrophyte biomass (R. J. Livingston, unpublished data). Instead, peak population densities at the two most heavily vegetated stations (E10 and E12) occurred during the reproductive season (March through July, Fig. 4). Few *R. naglei* were collected during the early part of this study at F12, but the amphipod became numerous from December, 1977 through February, 1978. Peak populations also occurred at E10 and E12 during the second winter season. Since reproductive activity of *R. naglei* did not extend into winter months the reason for winter peaks is left to speculation.

Ampelisca vadorum Mills 1963 (Ampeliscidae) was collected at all four stations but dominated the amphipod fauna at the unvegetated site (F11; 28% of the total). Abundance at Econfina 10 suggests that *A. vadorum* is capable of constructing its tubes in sediment heavily obstructed by seagrass rhizomes, but low numbers collected at the offshore stations indicate that the amphipod may prefer slightly broader salinity ranges available inshore. Peak abundances were observed between March and May (Fig. 3) although reproductive activity appeared to occur in all but the coldest months (Fig. 4). Mills (1967) found that *A. vadorum* in Barnstable Harbor, Massachusetts, breeds when temperatures exceed 8°C. The same relationship appears to hold in Apalachee Bay where the longer reproductive season in Florida is explained by latitudinal differences in temperature cycles.

Populations of *Ampelisca verrilli* Mills (1967) overlapped the distribution of *A. vadorum* in fine sands, as noted by Bousfield (1973). *Ampelisca verrilli* was the dominant amphipod (39.3%) at the unvegetated station (F11), but was rare at vegetated stations except during May at E10 (Fig. 3). Habitat requirements of this amphipod appeared to be similar to those of *A. vadorum*. Peak population densities occurred at the unvegetated site in April (813/m^2), corresponding with the beginning of reproductive season, April through August (Fig. 4). This species has a shorter reproductive season than its congener *A. vadorum* in Apalachee Bay; however, in Mississippi, Farrell (1970) found ovigerous *A. verrilli* throughout the year.

Lysianopsis alba Holmes 1905 (Lysianassidae) was one of the species which demonstrated considerable differences in seasonality at different stations (Fig. 3). At E10 (medium vegetation), *L. alba* was most abundant from April to September, corresponding with reproductive seasonality (Fig. 4). On the other hand, the amphipod was most abundant from July to January at F12 (low vegetation).

Populations were low at both E12 (dense vegetation) and the unvegetated site, Fenholloway 11. Also, annual variability in abundance patterns was demonstrated by low numbers of *L. alba* in the winter of 1977 and high numbers in the winter of 1978. *Lysianopsis alba* may preferentially inhabit seagrass beds where *Syringodium filiforme* is present since the amphipod was abundant at E10 and F12 and relatively rare at E12. The reason for two different seasonal patterns is unknown, but may be a result of differential predation or abundance of foods.

Carinobatea carinata Shoemaker 1926 (Bateidae) was most abundant and was present year round at the heavily vegetated station (E12); with peak abundance occurring in November through February 3 (Fig. 4). *Carinobatea carinata* was common only at stations with high biomass of *T. testudinum* (E10 and E12) and was limited to vegetated sites. Ovigerous females were collected only in February and March and in October and November (Fig. 4); therefore, winter peaks in population density may be reproductive.

Pontongenia sp. A (Pontogeneiidae) was approximately equal in abundance at all vegetated stations (Fig. 3), but rare at the unvegetated site. Amphipods of the genus *Pontogenia*, normally considered epifaunal and free-swimming, probably require shelter provided by vegetation. Populations were never high, but reached peaks ($350/m^2$) between August, 1977 and January, 1978. Since low numbers of ovigerous females were collected from August through October, peak populations were probably a reflection of reproductive activity. Very low abundances of *Pontogenia* sp. A prior to April, 1977, again illustrates the potential for wide annual variation in population densities.

Batea catharinensis Müller 1865 (Bateidae) was present year round at all stations in low numbers (Fig. 3). Density of vegetation appeared not to be important to the abundance of *B. catharinensis* as nearly equal numbers were collected at both the heavily vegetated site (E12) and the site with sparse vegetation (F12). Farrell (1970) found that this amphipod was associated with ectoprocts in Mississippi and its abundance may be more closely related to these animals than vegetation. Ectoproct data are not available for Apalachee Bay. Ovigerous females were collected during all but the coldest months in Apalachee Bay (Fig. 4), demonstrating a reproductive season longer than that reported by Bousfield (1973). Farrell (1970), however, found ovigerous specimens throughout the year in Mississippi Sound.

Synchelidium americanum Bousfield 1973 (Oedicerotidae) was most abundant at vegetated sites in Apalachee Bay despite infaunal burrowing habits of the species. *Synchelidium americanum* was most numerous in fall and winter collections (Fig. 3); however, such seasonality was not a reflection of reproductive activity. Ovigerous females were collected from April through September (Fig. 4).

Gitanopsis sp. A (cf. *G. tortugae*) (Amphilochidae) was numerically important only at stations Fenholloway 12 and Econfina 10; therefore, *S. filiforme* may be an important part of the animal's habitat. Populations were low at the other collecting sites, but this amphipod showed peak population densities at Econfina 12 (heavy vegetation) during the winter and early spring (Fig. 3) before fishes became numerous on the grass beds. Since *Gitanopsis sp.* A is konwn to be an

important prey species of pinfish (Stoner 1979b) fish predation may be an important limiting factor at E12. Population densities at the other two vegetated stations reflected periods of ovigery (May through September) (Fig. 4).

Melita appendiculata Say 1818 (Melitidae) was abundant only at station F12. No distinct seasonality of abundance was evident; however, the distribution of *M. appendiculata* was extremely patchy. All specimens taken on a single date were often found in a single core sample, suggesting aggregation by the species or a very specific microhabitat.

The only caprellid amphipod collected during this survey in Apalachee Bay was *Paracaprella tenuis* Mayer 1903. Although *P. tenuis* was probably undersampled by coring, it was most abundant at outer stations, F12 and E12, suggesting that the species is less euryhaline than most of the amphipods taken in this survey. *Paracaprella tenuis* is an epifaunal form, normally associated with seagrasses, sponges, hydroids and other living substrata (McCain 1968). Only four specimens were collected at the unvegetated site and those were associated with the red algae *Gracilaria* spp. The low number of animals collected did not permit evaluation of seasonality and no ovigerous females were taken.

Less than 100 individuals of each of 17 other amphipod species were collected; consequently, conclusions about seasonality of abundance are unreliable. Some information on habitat requirements of these species can be derived from abundance differences among stations (Table 2) and reproductive seasonality could be determined for some (Fig. 4).

DISCUSSION

All attempts to explain temporal patterns of abundance for individual amphipod species using multiple regression methods ended in failure when data on macrophytes and physical-chemical elements (e.g. salinity, water temperature, etc.) were incorporated as independent variables. Feeley (1967) and Nelson (1979a) also found that physical factors played a minor role in the regulation of amphipod abundances. Most of the amphipods collected in this study appear to be euryhaline and are reproductively active over wide temperature ranges. Although macrophyte biomass did govern spatial variation in the species composition and abundance of certain higher taxa in Apalachee Bay (Stoner 1980a), seasonality in benthic macrophytes was not particularly important in explaining temporal variability in amphipod abundance. Decreases in amphipod abundance with seasonal defoliation of seagrasses have been reported (Nagle 1968, Marsh 1973, Zimmerman 1978), but Nelson (1979a) found an inverse relationship of amphipod abundance and diversity with macrophyte biomass. From data provided in this report, it can be concluded that species probably have different responses to macrophyte biomass and linear relationships should not be expected.

Instead of associations with physical-chemical or macrophytic aspects of the habitat, abundances of individual amphipod species appeared to be most closely related to reproductive seasonalities (sometimes correlated with water temperature) and, in certain cases, to periods when fish predators were less abundant on

the grass beds. In general, ovigery of amphipods in Apalachee Bay occurred from March through November (exceptions being *A. vadorum*, *B. catharinensis*, *C. carinata*, and the *Corophium species*). This seasonality corresponds with the period during which water temperatures were greater than 15°C at the study area. Since much colder temperatures occurred from December to February, 15°C may be near the critical water temperature for reproductive activity and development of eggs. In all cases, reproductive seasons for amphipods collected in Apalachee Bay were as long or longer than those reported by Bousfield (1973) and most of those amphipods which were ovigerous at temperatures lower than 15°C are species frequently collected in the northern Atlantic (e.g., *A. vadorum* and *B. catharinensis*).

Abundance patterns not reflecting reproductive seasonality and the occurrence of local (station) differences in seasonal abundance within single species also suggest that patterns of abundance are far more complex than simple correlations with macrophyte biomass or physical characteristics of the habitat. Three explanations for local differences in abundance patterns are: 1) Reproductive seasonalities were different at the sampling sites, 2) requisite environmental elements such as particular microhabitats or foods were differentially available at the sampling sites, or 3) seasonal patterns of predator abundances or efficiencies were different locally. Because similar seasons of ovigery were found at all of the stations, the first explanation is unlikely. The second explanation is plausible, but research on the significance of microhabitats is required. As an example of how specific microhabitats affect amphipod distribution, Farrell (1970) showed that abundance of *B. catharinensis* was related to ectoproct abundance. Apparent aggregation of certain other species such as *M. appendiculata* and *E. levis* suggests that unknown small-scale microhabitat features may be important for them. Whether or not habitat preferences or associations are obligatory should also be examined.

The role of fish predation on amphipod populations probably varies with time and in space since abundance of pinfish and other predators of amphipods demonstrated temporal and spatial variation (Fig. 2 and Stoner, in prep. a). Also, the feeding behavior of *Lagodon rhomboides* is known to vary widely over both time and space (Stoner 1979b, 1980b). Those amphipods with seasonal abundance patterns that did not follow reproductive seasonalities were the species most heavily selected by the dominant amphipod-consuming fish in Apalachee Bay, *L. rhomboides*. For example, at the heavily vegetated station, *Lembos* sp. A had very high population density in the winter and a large decline in abundance, despite spring and summer reproductive activity, with the increase of fishes at the station in the spring. It was at this station that I found the highest degree of selectivity for the amphipod *Lembos* by pinfish (Stoner 1979b). At all three vegetated sites, *Lembos* populations increased when released from fish predation in November. Conversely, *L. rhomboides* consumed *C. compta* relative to its abundance at heavily and moderately vegetated stations (E10, E12) and appeared to reflect predatory pressure only when vegetation was sparse (F12). Populations did not increase after fish populations decreased in October and November at E10 and E12, suggesting that fish predation did not regulate abundance of this amphipod where

vegetation was heavy. Based on earlier work (Stoner 1979b) and data presented in this paper, other species which are probably influenced by fish predation include *R. naglei*, *B. catharinensis*, *Gitanopsis* sp. A and *P. tenuis*. Population density of *R. naglei* declined in June, somewhat later than other species apparently limited by predators. This occurrence is probably explained by the small size of *R. naglei* in the spring and early summer, which may permit its escape from fish predators at that time. Data from other studies also suggest that predation is an important component of amphipod population regulation (Young *et al.* 1976; Young and Young 1977, 1978; Nelson 1978; Van Dolah 1978). To date, however, only the influence of seagrass blade density on intensity of predation has been examined (Nelson 1979b). It is possible that alteration of prey choice with seagrass blade density or species composition may be as important as the influence on the intensity of predation. For example, recent experiments have shown that electivity of *Cymadusa compta* as prey by pinfish decreased significantly with seagrass biomass and that the electivity process was different in habitats composed of *Thalassia testudinum*, *Syringodium filiforme*, or *Halodule wrightii* (Stoner in prep. b).

Although the sampling program represented in this study was run for only fifteen months, variation in population abundance on an annual scale was also demonstrated (especially in *L. alba*, *R. naglei* and *Pontogenia* sp. A). As species undoubtedly have different temperature tolerances, the cold winter of 1977 and a mild winter of 1978 may explain some of the differences. However, *L. alba* is widely distributed along the Atlantic and Gulf coasts of the United States and in the Caribbean; therefore, temperature variation probably does not explain the annual variation in abundance patterns of that species. Annual variations in amphipod populations probably occur commonly in the field due to changes or extreme values in salinity, water turbidity, macrophyte biomass or species composition and reproductive success or distribution of predator species.

Plant biomass alone can be an important element of seagrass meadows which structures macrofaunal assemblages (Heck and Wetstone 1977, Stoner 1980a); however, subtle differences in the nature of the macroflora may govern abundance and distribution of individual species. I have shown that the majority of amphipods collected in this survey require vegetation, either through habitat preference or as a population response to predation. However, certain species such as *Elasmopus levis* and *Cymadusa compta* appear to be much more successful where microepiphytes are abundant on seagrass blades. Zimmerman (1978) showed that microepiphytes were an important food of certain amphipods including *E. rapax* and Nagle (1968) found that epiphyte-bearing blades of *Zostera marina* protected the amphipod *Microdentopus* from predation by killifish more effectively than *Z. marina* without epiphytes. Other amphipods collected in Apalachee Bay were most successful in unvegetated substrata (*Ampelisca vadorum* and *A. verrilli*), but only a few, relatively uncommon species occurred in both vegetated and unvegetated habitats (*Synchelidium americanum*, *Batea catharinensis*, *Corophium louisianum* and various species in the genera *Listriella* and *Stenethoe*). An analysis of fine-scale microhabitats will undoubtedly provide insight into the distribution of

amphipods. However, as illustrated in this paper, patterns in amphipod distribution and abundance are not simple functions of physical-chemical or macrofloral components of the habitat. Predators probably play an important role in both the distribution and abundance of certain amphipod species. The behavior of predators, however, is mediated by macrofloral elements of the habitat contributing to the complex interrelationships of predator, habitat and prey. Innovative experimentation is required to dissect the ecological machinery governing the distributions and abundances of animals in seagrass habitats.

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RESPONSES OF TRANSPLANTED AND INDIGENOUS *THALASSIA TESTUDINUM* BANKS EX KÖNIG AND *HALODULE WRIGHTII* ASCHERS. TO SEDIMENT LOADING AND COLD STRESS

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ABSTRACT

Observations of transplanted and indigenous *Thalassia testudinum* and *Halodule wrightii* were initiated in Redfish Bay, near Port Aransas, Texas, in July 1974 and continued until July 1979.

A total of 32 experimental plots were initiated (18 with *Halodule*; 14 with *Thalassia*). Twenty-three of these were planted prior to a dredging project begun in autumn 1975, 14.5 km distant from the experimental site (14 with *Halodule*; nine with *Thalassia*). The dredging project resulted in the addition of 15–25 cm of sediment to the site, covering the transplants and the *Halodule* meadow. By April 1976 *Thalassia* transplants were declining and dying back. Several of these plots were being invaded by *Halodule*. Following an extremely cold winter (1976–1977) *Thalassia* transplants disappeared and only *Halodule* plots remained. All introduced sediment finally washed out of the area by December 1977. Indigenous *Halodule* and most transplants decayed to form an organic silt layer 4–6 cm deep.

This study shows that *Thalassia* and *Halodule* can be debilitated by a sediment accumulation from even small dredging projects in this area. These effects are compounded when coupled with an extraordinary cold winter. *Thalassia* is much less tolerant to sediment loading and cold than is *Halodule*.

INTRODUCTION

One of the hypotheses underlying recent seagrass studies in the Seagrass Ecosystem Study (SES; NSF/IDOE Project of which I am a member) is that structural (plant factors such as morphology) and functional (such as adaptational response and nutrient cycling) gradients exist from the edge of a seagrass meadow to the center of that meadow. These gradients reflect the spatial and temporal development of that meadow.

Concentrated studies on the boundaries of meadows have particular importance especially if these boundaries are variable over a period of time. Kirkman (1978; Moreton Bay, Queensland, Australia), Dexter (1944, 1945, 1946, 1947, 1950; Massachusetts, USA), McMahan (1966; Lower Laguna Madre, Texas), den Hartog and Polderman (1975; Dutch Waddenzee), Jacobs (1979; Roscoff, France),

Orth (1976; Chesapeake Bay, Virginia, USA); and Wyer *et al.* (1977; Thames estuary; Great Britain) recorded such changes. Several of these studies detailed the changes in a specific meadow over a period of time. Such assessment if followed over a number of years could be an important tool in understanding the structural and functional interrelationships in seagrass species.

Species succession in the tropical seagrass system is documented (den Hartog 1970, 1973). The data indicate that *Halodule wrightii* is a pioneering-colonizing species which invades uncolonized substrates and is later replaced by the climax species, *Thalassia testudinum*, in the Caribbean and Gulf of Mexico. Also, if a *Thalassia* meadow becomes disturbed or adversely impacted, *Halodule* quickly invades the disturbed site (Phillips 1960).

Observations in this paper report the drastic changes in a *Halodule* meadow and transplants of *Halodule* and *Thalassia* in shallow water off the SW tip of Ransom Island in Redfish Bay near Port Aransas, Texas, from July 1974 to July 1979 (Fig. 1). These changes followed a dredging project begun in the Aransas Channel in autumn 1975, which resulted in an introduced sediment deposit of 15–25 cm during autumn 1975 on Ransom Is.

MATERIALS AND METHODS

Observations on the changes in an indigenous *Halodule* meadow were made as a part of a large seagrass transplantation project using *Halodule* and *Thalassia* in shallow water (15 cm deep at low tide; tide range ca. 0.5 m) at Ransom Is. in Redfish Bay. Maps of the inshore *Halodule* meadow were constructed from measurements to open spaces in the meadow and to the edge of an offshore *Thalassia* meadow from a fixed point on shore (Fig. 2). The distance from shore to the *Thalassia* meadow did not vary from 20 July 1974 to 3 July 1979 (period of the study).

From 22 July 1974 to 17 August 1976 a total of 18 *Halodule* and 14 *Thalassia* transplant plots were initiated at Ransom Is. Two *Thalassia* plots were located offshore near the indigenous *Thalassia* meadow (water one meter deep). Thirty plots of *Halodule* and *Thalassia* were initiated in the open spaces in the nearshore *Halodule* meadow. Due to the value of long-term analysis of seagrass transplants, only 23 of the total of 32 experiments will be reported in this paper. These 23 experiments were initiated prior to an introduced sediment load (autumn 1975; 14 *Halodule* plots; nine *Thalassia* plots).

The size of the open spaces in Fig. 2 is approximate. Diagrams of the *Halodule* meadow were made on most visits (20 July 1974; 13 Nov. 1974; 28 Jan. 1975; 8 Apr. 1975; 26 Aug. 1975; 16 Feb. 1976; 17 Aug. 1976; 21 Mar. 1977; 17 Dec. 1977; 10 July 1978; 3 July 1979).

Transplants were made using both cylindrical and rectangular plugs (cylinders 20 cm in diameter, 30 cm deep with seagrasses intact in the native sediment; cylindrical plugs were 317 cm^2 in area; rectangular plugs were 375 cm^2 in area) and turfs (shovelsful of seagrass intact in the native sediment; each turf was 0.1 m^2 in area). Each plot was 1.2 m $\times$ 1.5 m in area; plots using turfs were initially filled; plots using plugs were installed using three to six plugs per plot.

Seagrasses used in transplanting came from meadows at Ransom Is. (controls), at Fin and Feather (*ca* 2 km distant), and from Upper Laguna Modre (Fig. 1).

RESULTS

From 20 July 1974 (initial observation) through the observations made on 21 March 1977 (Fig. 2A-E) the boundaries of the *Halodule* meadow at Ransom Is. remained relatively constant. Most changes were beneficial in that the open spaces in this meadow gradually filled in with expanding *Halodule*. The offshore

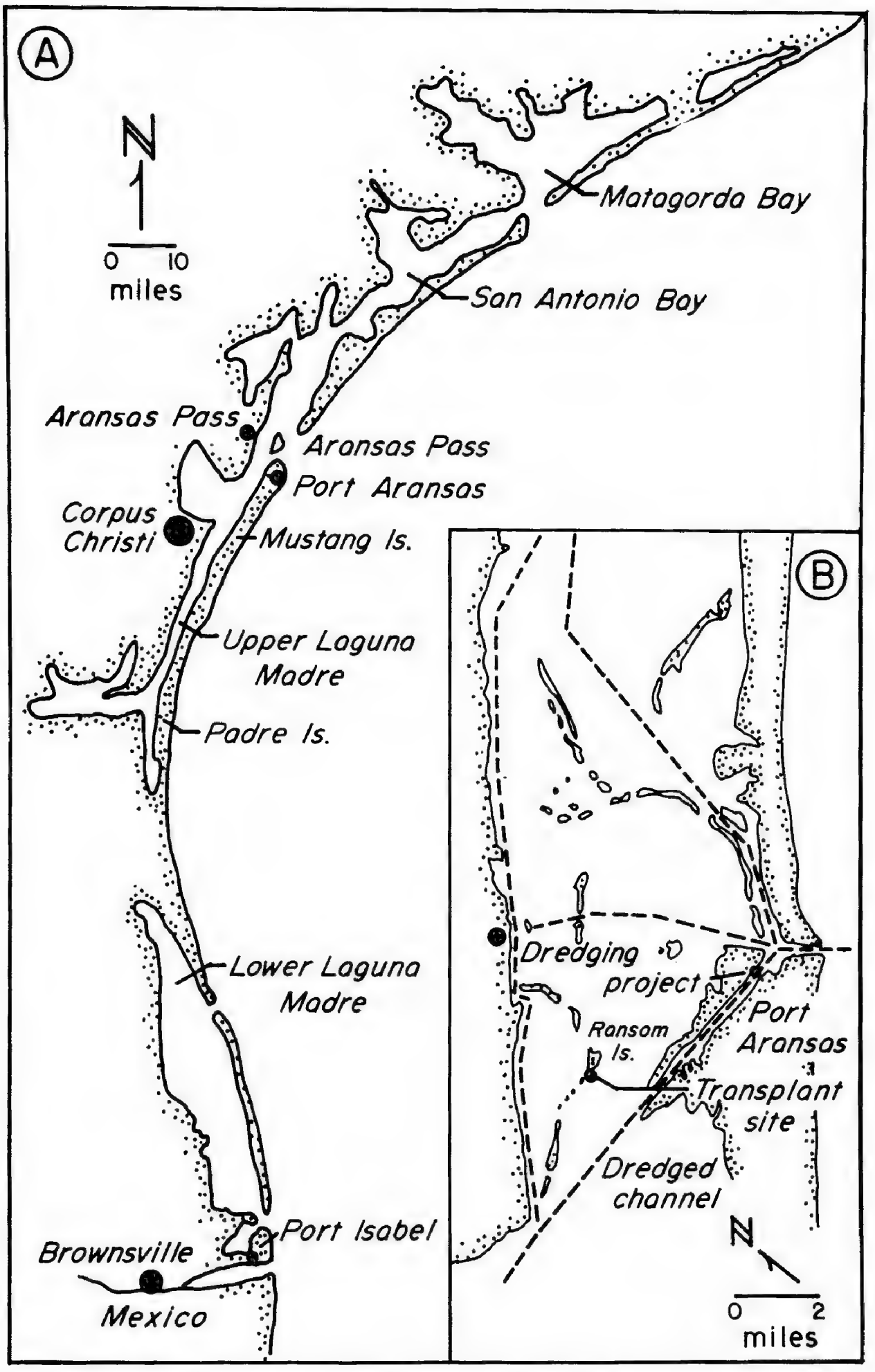

FIG. 1. Map of area. A. Coastline of southern Texas; B. Map of local area.

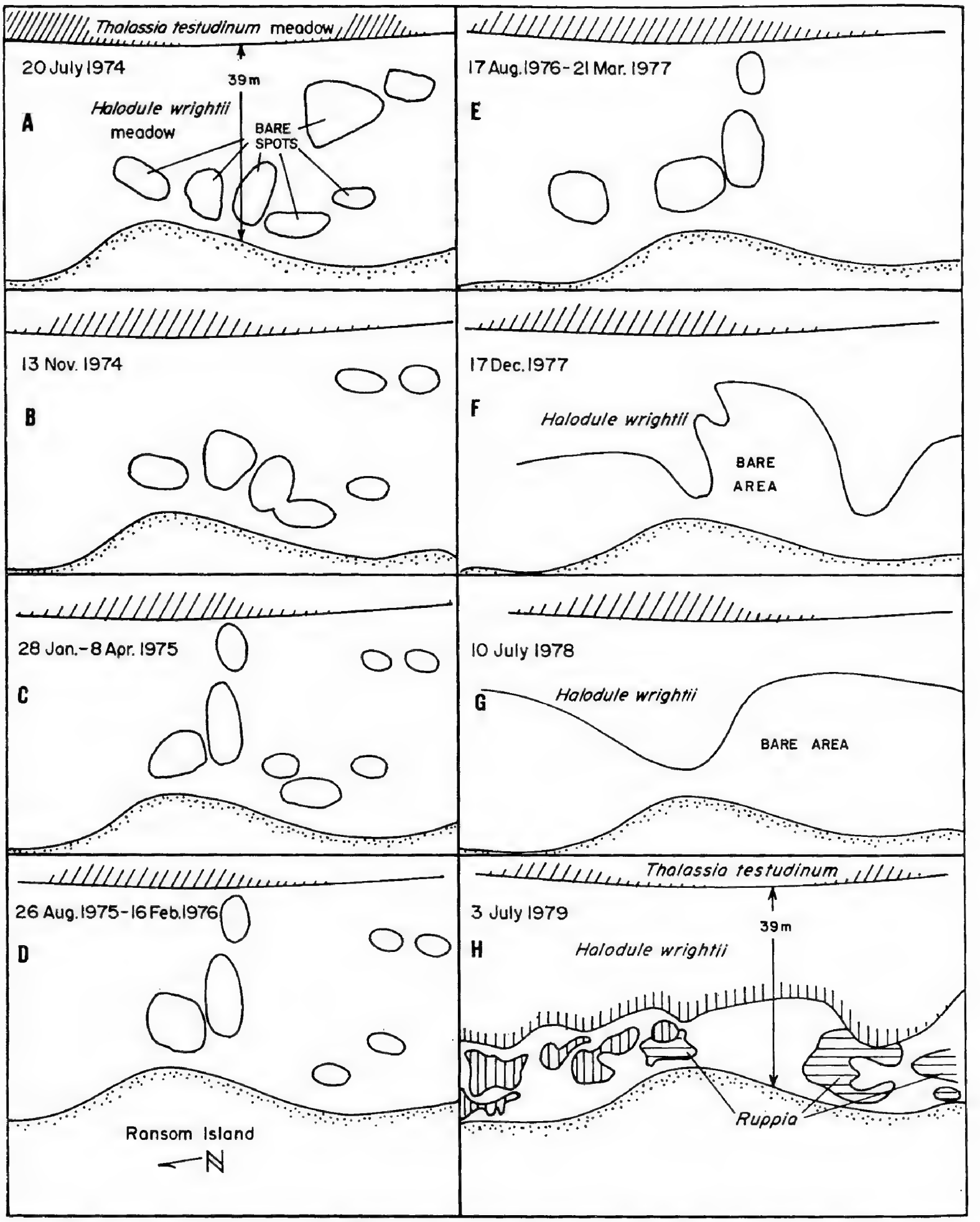

FIG. 2. Transplant site at SW corner of Ransom Island in Redfish Bay, showing relationship between native *Halodule* meadow, offshore *Thalassia*, bare spots in *Halodule* and transplant plots.

A. 20 July 1974
B. 13 Nov. 1974
C. 28 Jan. and 8 Apr. 1975
D. 26 Aug. 1975 and 16 Feb. 1976
E. 17 Aug. 1976 and 21 Mar. 1977
F. 17 Dec. 1977
G. 10 July 1978
H. 3 July 1979

border between *Halodule* and *Thalassia* remained a relatively straight line, i.e., parallel to the shore.

Observations made on transplanted *Halodule* and *Thalassia* on Ransom Is. from 20 July 1974 through August 1975 showed that most transplants using both plugs and turfs were surviving (20 plots; 23 plots established; Table 1)[1] (two *Halodule* plots dead; one *Thalassia* plot dead—one of two placed offshore in water one meter deep). All 20 plots showed vigorous plants with extending rhizomes which were joining plugs or in the turf plots were escaping their boundaries. On 15 February 1976 17 plots contained living plants (11 *Halodule*; six *Thalassia*). On 21 April 1976 16 plots showed surviving plants (10 *Halodule*; six *Thalassia*), but all remaining *Thalassia* transplants were selectively losing vigor, i.e., declining in shoot numbers and bottom coverage. The second *Thalassia* plot originally placed in water one meter deep expired before 21 April 1976 (located near offshore indigenous *Thalassia*). On 16 August 1976 all *Thalassia* plots were being invaded by surrounding *Halodule* (only four *Thalassia* plots remained in Aug. 1976; these showed dying or further declining growth; 10 *Halodule* plots remained). *Halodule* and *Thalassia* transplants were not harmed during the first normal winter of 1974–1975. After one year (July 1974–Aug. 1975) all transplants were vigorously expanding.

Between 26 Aug. 1975 and 15 Feb. 1976 15 cm to 25 cm of sand and silt were deposited over the inshore *Halodule* meadow and transplants at Ransom Is. This sediment was not deposited on the offshore indigenous *Thalassia*, which did not appear to be impacted at all. The only activity which appeared capable of raising such a load was a dredging project begun in the Aransas Channel in autumn 1975. No unusual rains or winds occurred during this period. *Thalassia* transplants were severely impacted by the sediment.

Following the coldest winter in recent history in Texas (at least two cold spells in January 1977 with air temperatures at or below −1°C), most plots showed dead plants on 21 March 1977 (only four plots of 23 established by that date showed living plants, all *Halodule*). On 17 Dec. 1977 only two of these plots contained living plants (Table 1). On 10 July 1978 the same two *Halodule* plots showed living plants. The indigenous *Thalassia* showed extensive leaf kill following the cold winter of 1976–1977, but all rhizomes and erect short shoots were living.

On 21 March 1977 the sediment load still covered the inshore *Halodule* meadow. By 17 Dec. 1977 all the introduced sediment had completely washed off, but in its place was a layer of black ooze, 4–6 cm deep, produced by the decay of the indigenous and transplanted *Halodule*. The indigenous *Halodule* meadow at Ransom Is. was still intact on 21 March 1977 (after the cold winter; Fig. 2E), but had been greatly impacted and had receded by 17 Dec. 1977 (Fig. 2F) following the removal of the sediment load.

The sediment covered the transplants and indigenous *Halodule* at Ransom Is. for at least 13 months, perhaps as long as 21 months (Feb. 1976 to Dec. 1977), or even longer (autumn 1975 to Dec. 1977).

[1] The extensive data documenting all transplants are held by the author.

TABLE 1

Response of Transplanted *Halodule* and *Thalassia* to Sediment and Cold.

Species	Survival of Transplants					
	Before Sediment Deposit (observed on 26 Aug 1975)		After Sediment Deposit (observed on 16 Aug 1976)		After Cold Winter (1976-77) (observed on Dec 1977)	
	Turf	Plug	Turf	Plug	Turf	Plug
Halodule wrightii (6 turf plots-8 plug plots established between 20 July 1974 and 26 Aug 1975)	5	7	5	5	1	1
Thalassia testudinum (4 turf plots-5 plug plots established between 20 July 1974 and 26 Aug 1975)	4	4	2	2	0	0

The impacts of this introduced sediment which weakened and led to the demise of the *Thalassia* transplants and perhaps the transplanted and indigenous *Halodule*, coupled with the cold winter of 1976–1977, were finally observed on the final visits (Fig. 2G–H).

By 10 July 1978 (Fig. 2G) the indigenous *Halodule* meadow was beginning a recovery. On 3 July 1979 (Fig. 2H) numerous *Ruppia* patches were growing inshore of the recovering *Halodule*.

During the study period transplanted *Halodule* and *Thalassia* showed ameliorating morphological growth responses. Most of the transplanted *Thalassia* short shoots produced new horizontal rhizomes, some producing new short shoots from these new growing tips (Fig. 3) (I have observed this in indigenous *Thalassia* from Texas to the Florida Keys; cf., Tomlinson and Vargo 1966; Tomlinson 1974). The transplanted *Halodule* responded to an increasing sediment load by orienting new rhizome growth upward toward the sediment surface. This upward growth occurred over the entire rhizome mat. *Halodule* rhizomes are normally situated from 2–5 cm deep in the substrate. *Thalassia* rhizomes may occur from 10–25 cm deep or even deeper, depending on the sand content and substrate firmness (personal observation).

DISCUSSION

Most *Halodule* transplants and the indigenous *Halodule* meadow survived for a minimum of 13 months following an introduced sediment load of 15–25 cm in autumn 1975 which covered the plants. Remaining plants did not die until after an extremely cold winter (1976–1977). *Thalassia* transplants were selectively but conspicuously impacted by the sediment loading alone (some died outright; all others showed declining plant numbers and dying growth). The data also suggest that the extremely cold winter of 1976–1977 following the long period of sediment loading in 1975–1976, exceeded the ability of *Halodule* to survive both impacts.

Kirkman (1978) documented a conspicuous decline in seagrass growth in Moreton Bay, Queensland, Australia. He showed that sand moving onto the grass bed

FIG. 3. *Thalassia testudinum* showing rhizome and new short shoot arising from meristem on old short shoot, ca. 3.5 cm above older horizontal rhizome. Plant transplanted on 28 Jan. 1975; photo taken on 17 Feb. 1976.

was the primary cause of the decline. Eleuterius (1974), working in Mississippi Sound, found that sediment deposition rates > 5 cm/month exceeded the growth rate of *Halodule*; rates > 2.5 cm/month exceeded the growth rate of *Thalassia*. When this happened, plants died.

Except for two plots of transplanted *Thalassia* located in deeper water near the indigenous meadow (one died before the introduced sediment; the other died immediately after), all other transplants were located inshore in the more shallow *Halodule* zone. Considering that transplanted *Thalassia* in this zone showed vigorous growth up to the sediment loading in autumn 1975, I conclude that the species had an adaptive tolerance to normal conditions in that zone. However, *Thalassia* is probably limited to a deeper offshore location due to intolerance to occasional extremely cold water and sedimentation. The adaptive tolerance of *Halodule* to cold water and sediment loading appears to be broader than that of *Thalassia*. The data support the gradient hypothesis of seagrass species succession: *Halodule* is a pioneering species with broad adaptive tolerances; *Thalassia* is a climax species but with a more restricted tolerance range. Phillips (1960) demonstrated that *Halodule* can quickly invade a disturbed *Thalassia* meadow. Thus, the invasion of *Halodule* into the declining *Thalassia* plots (observed on 16 Aug. 1976) indicated that the *Thalassia* was adversely impacted.

Odum (1963), working in Redfish Bay, Texas, found that *Thalassia* productivity was reduced by diminished photosynthesis following dredging in a nearby channel. The dredging released silts which reduced light penetration in the water. Within a year *Thalassia* growth in the same area was exceptional. He reasoned that dredging of the sediments may have stimulated long-term plant growth by releasing nutrients to the water column. He concluded that dredged materials discharged in only 0.5 m of water or less may shoal the water depth critically over a much wider zone than where the water is one meter to three meters deep.

The presence of *Ruppia* close to shore was noted by Humm (1956) in Mississippi Sound and by Simmons (1957) in Upper Laguna Madre, Texas. These observations as well as those by Phillips (1960) in Florida and Hoese (1960) in Texas indicate that the appearance and growth of *Ruppia* inshore of *Halodule* are not so much a function of zonational factors (desiccation, osmotic stress, temperature stress) as a reaction to lowered salinity, i.e., the area nearest the shore (closest to terrestrial runoff) showed the greatest reduced salinity.

This study shows that dredging projects in Redfish Bay, Texas, may constitute a serious threat to seagrass survival. Seagrasses grow to a depth of only two meters in Redfish Bay (personal observations; summer 1978). This distribution is probably a result of constant winds which stir up bottom silts and create almost constant turbid water. *Halodule* occurs only in water 0.5 m deep or less. Progressive shoaling in these meadows will result in shoaling further offshore in the deeper *Thalassia* growth. Increased dredging, if accompanied by unpredictable severely cold winters, could result in the disappearance of seagrasses from bays in this area.

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HEAVY METAL ACCUMULATION BY SELECTED *HALODULE WRIGHTII* ASCH. POPULATIONS IN THE CORPUS CHRISTI BAY AREA[1]

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ABSTRACT

Leaf and (root + rhizome) contents of Cd, Zn, Cu, Fe, Mn and Ni, were measured on a seasonal basis in the seagrass, *Halodule wrightii* Asch., collected from seven locations in the Corpus Christi, Texas area. *Halodule* was well-established (summer standing crop at least 200 g dry wt/m^2) at these sites, which represented a gradient of habitats ranging from Redfish Bay near Port Aransas to Corpus Christi Bay near the mouth of Nueces Bay. Seagrass tissue contents of the six metals showed a positive correlation with sediment levels, and two- to five-fold elevated Cd and Zn were consistently found in plants at contaminated sites in Corpus Christi Bay, compared to plants at control sites in Redfish Bay. Implications of these findings are discussed in relation to food chain transfer of heavy metals.

INTRODUCTION

Alarmingly high zinc and cadmium concentrations were reported by Holmes *et al.* (1973) in sediment samples from some parts of Corpus Christi Bay. These contaminated sediments were attributed to heavy metal migration, primarily due to winter storms, from the Corpus Christi, Texas inner harbor industrial area and redistribution to the open bay system. Since this bay system is very productive as a commercial shrimping and fishing area, the extent of incorporation of these heavy metals into local food chains is a highly pertinent question.

Extensive beds of submergent seagrasses occur in the Corpus Christi/Redfish/Aransas Bay area. Several studies indicate that these rooted macrophytes are major primary producers in a number of detritus-based food chains (Fenchel 1970, Harrison 1977, Fry and Parker 1979). Because seagrasses possess functional angiosperm root systems (Tomlinson 1969, Bristow and Whitcombe 1971), they may accumulate heavy metals from contaminated sediments. The potential of cordgrass (*Spartina alterniflora*) for mediating the transfer of heavy metals to food chains is well-known (Williams and Murdoch 1969, Drifmeyer and Odum 1975); and this work provides a good model for seagrass ecosystems such as those in Corpus Christi Bay. Acting as a "pump," *Spartina* concentrates heavy metals

[1] University of Texas Marine Science Institute Contribution No. 401.

from reducing sediments and the toxic metals are then readily available to the biota via detritivore food chains (e.g. shrimp). This type of mobilization and transport of heavy metals from estuarine sediments has been postulated (Burrell and Schubel 1977) for seagrasses, but little documented evidence exists.

These factors prompted a comparative study of heavy metals in the seagrass, *Halodule wrightii* Asch., from different sites in the Corpus Christi Bay system. A sampling scheme was designed so that a gradient of impacted plant populations was analyzed, ranging from Gulf-influenced Redfish Bay plants near Port Aransas, Texas to Corpus Christi Bay plants, directly exposed to river and industrial discharges, at Nueces Bay Causeway near Corpus Christi, Texas. Simultaneous measurements of heavy metals in sediments and water column were made for correlation with plant tissue contents. The data document the positive correlation between seagrass tissue content and sediment concentration of cadmium in this bay system.

MATERIALS AND METHODS

Figure 1 shows the location of the seven sites where stands of *Halodule wrightii* were sampled. These sites were chosen because *Halodule* was abundant (extensive beds with early June biomass 200–600 g dry wt/m^2) and plants were always subtidal (0.3 to 1.0 m water depth). One Laguna Madre site was included as a control site.

Seagrass samples were collected at all seven sites three times during the 1979 growing season: late March, early June, and early September. In early November, an additional set of samples was taken at the Indian Point and Redfish Bay sites 2, 3, 6 and 7. Sediment and water samples were collected once, during the late spring sampling period.

Several plant samples at each site were collected within an area of 10–20 m^2 and pooled to give one sample for analysis, thus eliminating local variations between samples. Pooled samples were returned to the laboratory in plastic bags containing seawater. Within 12 hours of collecting, all plants were hand cleaned of epiphytes, rinsed quickly two times in twice deionized water, separated into leaves and underground (roots + rhizomes) portions, and dried in an oven at 70–80° C for 7–10 days between pieces of filter paper. Pooled sediments from each site were dried at the same temperature and pulverized with a mortar and pestle.

Trace metal analysis involved acid digestion of dried samples. Approximately 0.6–1.0 g plant material was digested with a 4:1 mixture of Ultrex nitric acid:perchloric acid for 36–48 hrs. Sediment samples (1.0 g) were digested with Ultrex nitric acid for 24 hr. After taking samples almost to dryness, they were dissolved in 1 N HCl, filtered through Whatman No. 40 paper, and diluted to 10 ml. This solution was analyzed by flame atomic absorption spectrophotometry for Fe, Mn, Zn, Cu, Ni and Cd using a Perkin-Elmer 303 instrument.

Matrix interference was negligible when evaluated on some samples for Cd, Ni and Zn by using the method of standard additions. Background corrections for non-specific absorption were routinely determined using the following non-absorbing lines for each metal: Fe, 247.3 nm; Zn, 220.2 nm; Cu, 322.9 nm; Ni, 231.6 nm; and Cd, 226.5 nm.

The precision of the technique appears good based on the variation in replicate analyses on the same sample. The percent deviation for each metal was Fe, 4%; Mn, 2%; Zn, 7%; Cu, 3%; Ni, 9%; and Cd, 8%.

The accuracy of the technique was checked by analyzing NBS orchard leaves (#1571) reference material. When 0.6 g samples were carried through the same procedure as seagrass samples, the results for Fe, Mn, Cu, Zn and Ni were all within 10% of the NBS certified values. For Cd, the value obtained was 20–30% lower than the standard.

Water samples were returned to the laboratory in acid-washed plastic bottles on ice and, within 3 hr of collecting, filtered through 0.4 μm Nucleopore filter and acidified with 10 ml conc. HCl

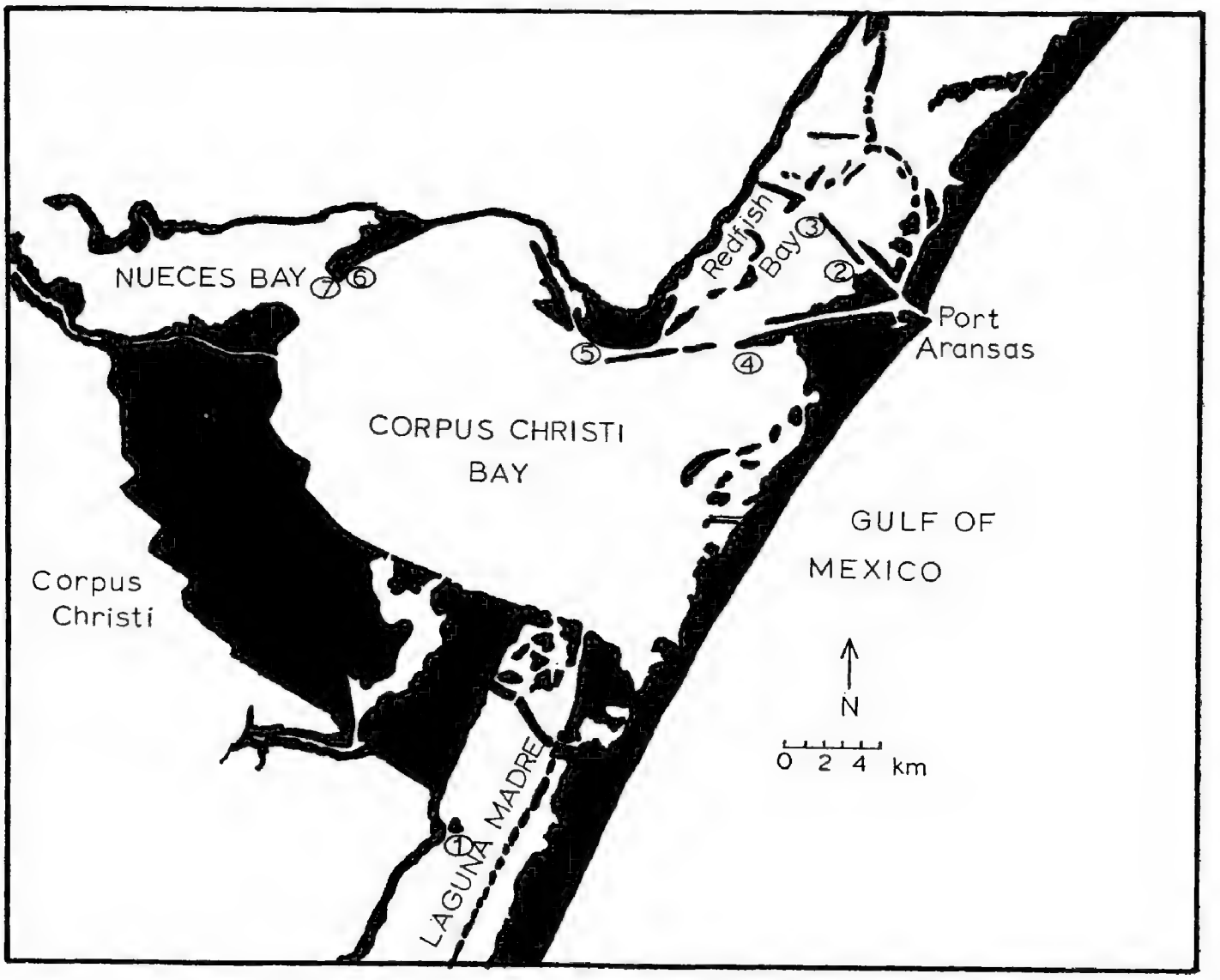

FIG. 1. Map of bays in vicinity of Corpus Christi, Texas, showing location of seven collecting sites. Sites are numbered 1 through 7. Exact locations are: Site 1, Laguna Madre near Pita Island; Site 2, Redfish Bay south of Harbor Island; Site 3, Redfish Bay east of Stedman Island; Site 4, East Flats area of Corpus Christi Bay; Site 5, Corpus Christi Bay at Ingleside Point; Site 6, Corpus Christi Bay, northeast of Indian Point; Site 7, Corpus Christi Bay, northwest of Indian Point.

per liter. The soluble trace metals were concentrated by passing the sample through Chelex 100 ion exchange resin (Bio-Rad Inc.) previously washed with 4N NH_4OH. The seawater was adjusted to pH 7.6 with NaOH, and passed through the column at a flow rate of 4 ml per min. The adsorbed metals were eluted from the column with 4N HNO_3 and the eluate evaporated to dryness. The dried sample was then made up to 10 ml volume with 1N HCl and trace metals analyzed by atomic absorption as described above.

RESULTS

Trace Metals in Sediments

Table 1 presents data on trace metals content of sediments from two depths at several of the collecting sites. The sediments at the Indian Point sites contain substantially more Mn, Zn, Cu and Cd than other areas, although the amount varies with the individual metal. Cadmium is nine times higher at Indian Point, and four times higher at Ingleside, than at the Redfish Bay sites. The latter site has twice as much Cd as the Laguna Madre site.

TABLE 1

Concentrations of heavy metals in surface and subsurface sediments of *Halodule wrightii* grassbeds in vicinity of Corpus Christi, Texas. Values are means ± range for three determinations, in μg/g dry wt sediment.

Location	Fe	Mn	Zn	Cu	Ni	Cd
Laguna Madre (Pita Island)						
0 - 6 cm	1600±325	22±5	4.0±0.3	1.6±0.2	3.0±0.3	0.04±0.01
6 - 12 cm	1250±120	18±3	10.2±0.9	1.7±0.3	2.5±0.4	0.06±0.01
Redfish Bay (near Stedman Is.)						
0 - 6 cm	2910±270	30±3	17.2±1.5	1.8±0.2	8.1±0.8	0.10±0.03
6 - 12 cm	3690±315	36±5	22.1±0.9	2.2±0.5	5.7±0.6	0.14±0.03
Corpus Christi Bay (Indian Point)						
0 - 6 cm	3350±185	57±5	88±4.0	6.2±0.5	7.8±0.5	0.94±0.10
6 - 12 cm	4070±370	60±7	92±6.0	7.0±1.1	11.8±0.8	1.24±0.22
Corpus Christi Bay (Ingleside Pt.)						
0 - 6 cm	3520±270	44±4	45±2.0	5.9±0.3	9.0±0.8	0.42±0.07
6 - 12 cm	3810±510	42±2	47±5.0	5.8±0.7	9.2±0.9	0.48±0.10

Iron was similar for all areas except Laguna Madre, which has about one-half that of the other areas. When considered in relationship to iron content. the sediments from the Corpus Christi Bay areas (i.e. Indian Point and Ingleside Pt.) are enriched in varying degrees with the heavy metals Mn, Cu, Zn and Cd, compared to Redfish Bay sites. When these results for 1979 are compared with the data of Holmes *et al.* from 1974, elevated levels of Cd and Zn in upper Corpus Christi Bay sediments are still apparent some 8 years later. However, the low levels of Zn, Cu and Cd at the Redfish Bay and Laguna Madre sites appear similar to San Antonio Bay sites examined by Trefry and Presley (1976), who felt that no heavy metal pollution was indicated for San Antonio Bay.

Trace Metals Dissolved in Water

Soluble trace metals at the sites were generally similar (Table 2). All concentrations were in the low ppb range, and Zn and Cd appeared within the limits for normal coastal waterways (Brooks 1977), although a measurement on one day may miss a pulse load of metals. These data provide some evidence that sediment levels of metals do not significantly affect the disssolved levels in the open bay.

Trace Metals in *Halodule* Leaves

Leaf metal data reveal that leaf Fe correlated with leaf contents of Zn, Cd and Cu. When plants showed high Fe values, they also exhibited high levels of these other heavy metals. A sample correlation plot of leaf Cd vs. leaf Fe demonstrates

TABLE 2

Concentrations of heavy metals dissolved in sea water at study sites in Corpus Christi, Texas area on May 30, 1979. Values are average of two determinations ± range, in μg/1.

Study Site	Fe	Mn	Zn	Cu	Ni	Cd
Laguna Madre, (Pita Island)	< 0.2	16.0 ±1.0	15.0 ±1.0	2.5 ±0.5	10.8 ±0.9	0.6 ±0.2
Redfish Bay (near Stedman Is.)	< 0.2	4.5 ±0.5	10.2 ±0.8	1.5 ±0.4	9.0 ±0.6	0.4 ±0.2
Corpus Christi Bay (Indian Point)	0.3 ±0.1	2.0 ±0.4	15.2 ±1.3	0.9 ±0.3	13.9 ±1.2	0.6 ±0.3

the high degree of positive correlation ($r = +0.78$) between the two metals (Fig. 2). A similar correlation can be made for leaf Cd, Zn or Cu vs. sediment content of these metals.

Figures 3 and 4 show that Indian Point leaves contained the highest levels of Fe, Zn, Cd and Cu, followed in order by Ingleside Pt., Laguna Madre, East Flats

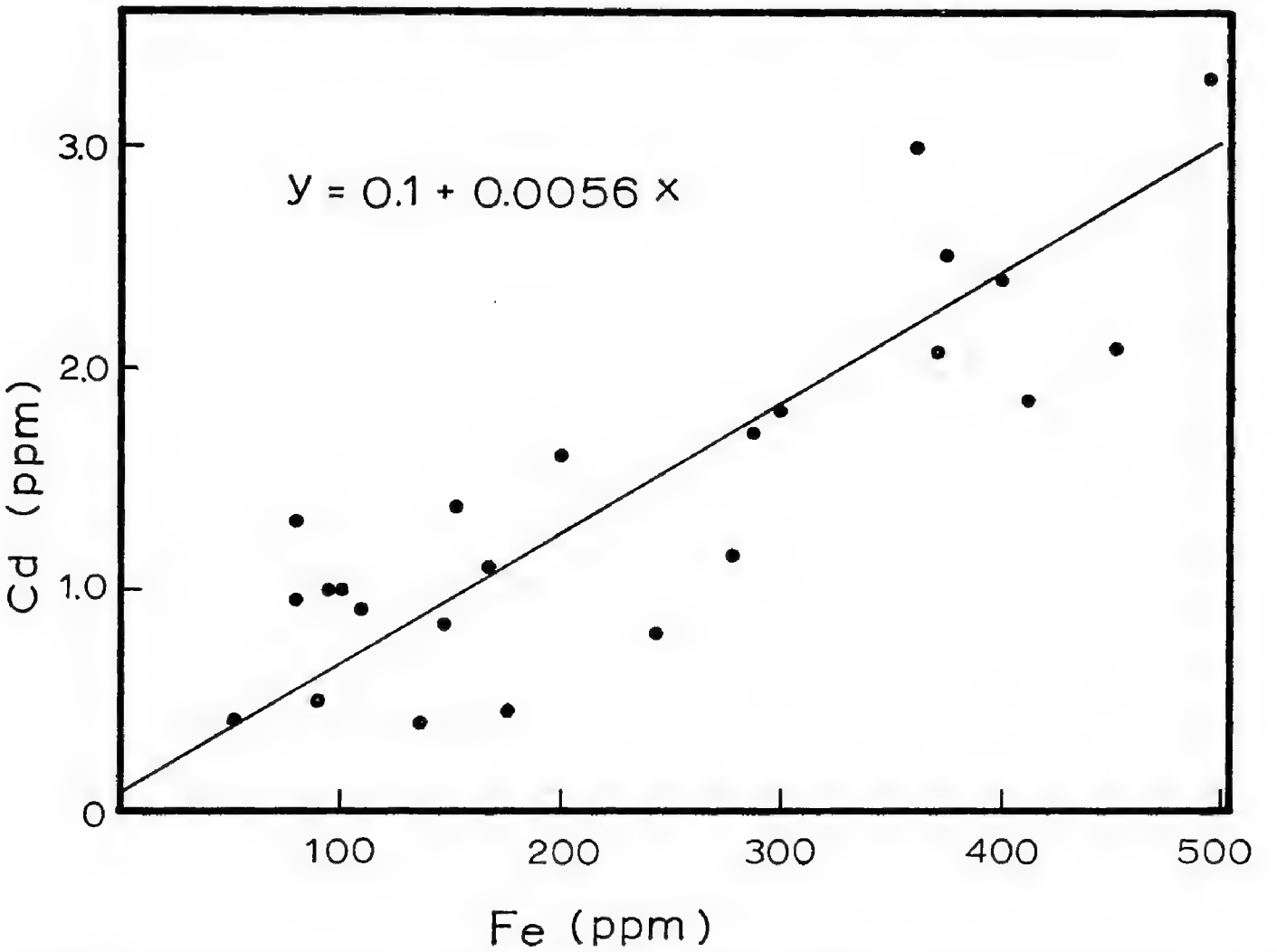

FIG. 2. Fe vs. Cd scatter plot for *Halodule wrightii* leaves collected at the seven sites over all seasons.

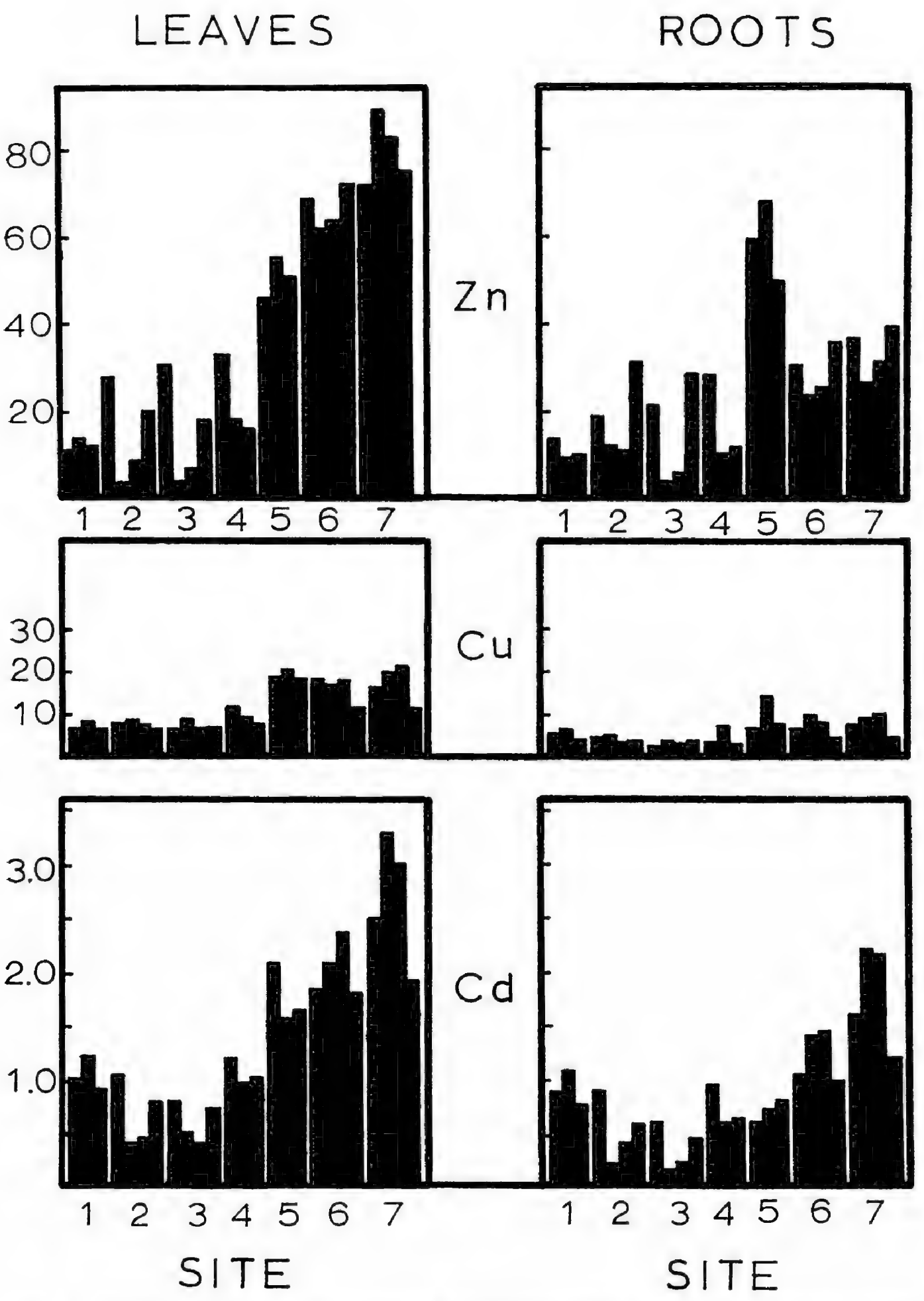

FIG. 3. Seasonal variation in zinc, copper and cadmium content of *Halodule wrightii* collected at the seven sites in the Corpus Christi, Texas area. Leaf and (root + rhizome) fractions were analyzed separately. Collecting sites, described in Fig. 1, are designated by numbers 1 through 7 under each bar graph. For all sites, three values are given (left to right): the late March value, the late May–early June value, and the early September value. For sites 2, 3, 6 and 7, an addi-

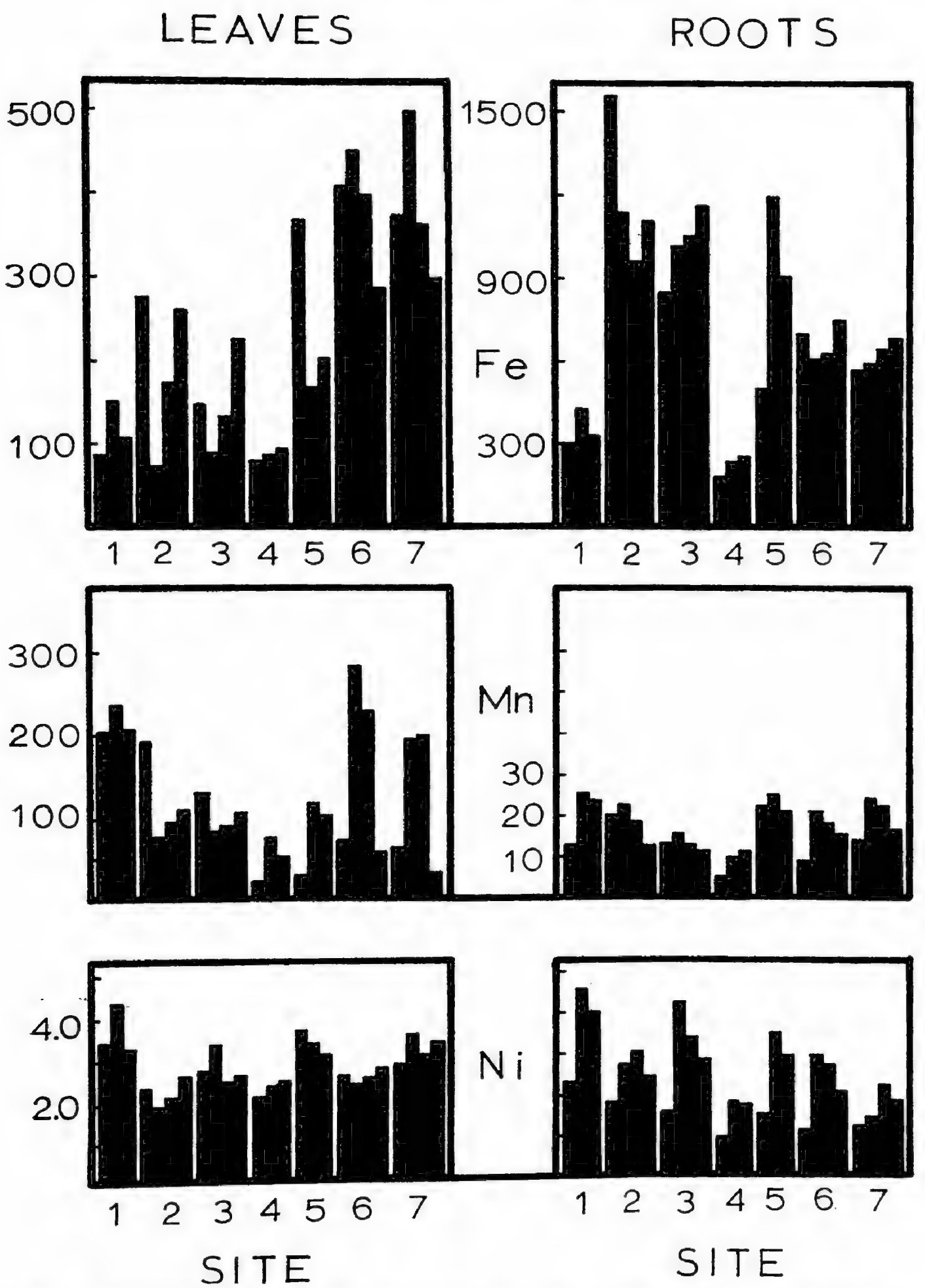

FIG. 4. Seasonal variation in iron, manganese and nickel content of *Halodule wrightii*. All other details same as for Fig. 3.

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tional value, that for late October, is also given. All samples for one season were collected over at most a seven day period. Data, in μg/g dry wt., are averages of two replicate analyses.

and Redfish Bay leaves. Zinc and cadmium in the plants exhibit a steady increase as one moves from the Redfish Bay area, up the ship channel past the East Flats area, past Ingleside out into Corpus Christi Bay, and over to Indian Point at the juncture of Corpus Christi and Nueces Bays. This trend is most pronounced during the peak of the growing season (June to September) when Indian Point samples showed five times more Cd in leaves, and ten times more Zn, than Redfish Bay plants.

On a seasonal basis, the Redfish Bay and Corpus Christi Bay sites displayed extremes in accumulation patterns for Fe, Mn, Zn and Cd (Figs. 3 and 4). At one extreme, the Redfish Bay plants showed 2- and 3-fold higher levels of Fe, Mn, Zn and Cd during the early spring than later in the growing season (June–Sept.). However, by the beginning of November, the dormant season when growth rates of plants have slowed down, there was a definite increase in tissue levels. Conversely, at Indian Point sites, the levels of Fe, Mn, Zn and Cd in plants increased 30–40% later on during the growing season compared to early spring values. However, by the beginning of November, there was a definite decrease in the tissue levels of these same metals. This behavior for tissue levels of Fe, Mn, Zn and Cd had the effect of magnifying the difference between Redfish Bay and Indian Point plants at the peak of the growing season.

The Laguna Madre site was unusual in some respects, possibly reflecting the environmental stimulus of hypersalinity. While leaf Fe was quite low (as low as Redfish Bay sites), leaf Cd was significantly higher than Redfish Bay (twofold), similar to East Flats, but still much lower than Indian Point. Leaf Mn was much higher than all other sites except Indian Point, while leaf Zn was low, similar to Redfish Bay sites.

Trace Metals in *Halodule* Roots

Root data generally followed the patterns observed for leaves with respect to Zn, Cd and Cu (Figs. 3 and 4). Overall concentrations of metals were uniformly lower (20–50%) than for leaves, except for Zn in Ingleside Pt. roots. Indian Point root samples contained the most Zn, Cd and Cu, followed by Ingleside Pt., East Flats and finally, Redfish Bay roots with the least.

Trace Metals in *Ulva*

Concentrations of these same trace metals were compared for the macrophytic green algae, *Ulva lactuca*, and *U. fasciata* growing at the Indian Point site and at the South Jetty in Port Aransas, Texas (Table 3). Since trace metals are obtained by *Ulva* strictly from the water column, levels in this alga will depend on and reflect ambient soluble metal concentrations. Fe and Mn were more abundant in Indian Point algae, similar to Indian Point *Halodule*, whereas Cu was higher in South Jetty algae, opposite to the situation with Indian Point *Halodule*. Therefore, it is significant that levels of Zn and Cd in *Ulva* from the two widely-separated sites were almost identical and low, reflecting the supposedly pristine S. Jetty site. These data provide more evidence that the Cd and Zn levels in *Halodule* at Indian

TABLE 3

Concentrations of heavy metals in *Ulva* species collected at two sites during 1979. Values are average of two determinations, in μg/g dry wt.

Species and Sites	Fe	Mn	Zn	Cu	Ni	Cd
Ulva lactuca (collected late March)						
South Jetty	102	20	57	12.5	5.3	0.30
Indian Point	1800	28	55	8.5	6.7	0.22
Ulva fasciata (collected mid June)						
South Jetty	245	29	80	12.5	6.1	0.60
Indian Point	1200	45	40	7.5	6.0	0.38

Point result from sediment conditions rather than dissolved levels, whereas Fe and Mn may in fact be influenced by dissolved metal concentrations.

DISCUSSION

Concentrations of trace metals in plants result from uptake in response to (1) ambient levels of available metals and (2) metabolic requirements for metals. For Fe, Mn and Zn, essential metals which function in various physiological processes, fairly high tissue levels may be accumulated at low ambient concentration if there is a metabolic requirement for that metal. Conditions which affect the growth rate of the plants (such as macro-nutrient supply, light intensity, sediment type, turbidity of water, temperature, salinity, etc.) may lead to build-up of these essential metals. Therefore, high levels of essential metals in seagrasses may indicate "luxury" consumption of the metal rather than "pollution" of an area.

Contamination by cadmium can be easily assessed however, since uptake reflects solely ambient environmental levels. Unlike the previously mentioned metals, Cd is not essential and is much more toxic than they are at much lower levels (Brooks 1977). Toxicity to some zooplankton has been demonstrated at ambient dissolved levels of 5 ppb (Bertram and Hart 1979). Cadmium once taken up is tightly bound in cells probably as a stable metallothionein-like protein (Bertram and Hart 1979). It is not readily excreted and remains in tissues (Brooks 1977).

The cadmium level of *Halodule* from this study can be compared to Cd levels measured by Foster (1976) in various brown algae from polluted areas in England and by Stenner and Nickless (1975) from heavily polluted waters on the Atlantic coast of Spain and Portugal. Foster found Cd to range from 1.5 to 2.1 ppm in *Fucus vesiculosus* and *Ascophyllum nodosum*; Stenner and Nickless measured up to 3.2 ppm in *Fucus* sp., 2.0 ppm in *Ulva lactuca*, and 7.4 ppm in *Enteromorpha* sp. This compares to the level of 2–3 ppm for *Halodule*. These algae differ from *Halodule* in one important aspect. Dry weight of *Halodule* is 35% of the wet weight compared to ca 20% for the algae; thus the total Cd contained in *Halodule* biomass could actually be higher by a factor of ca 50%, when compared to the macro-algae biomass.

Cadmium uptake by plants appears to be regulated by the Zn:Cd ratio in the environment (Sidle *et al.* 1976), and Cd uptake may be suppressed by a high Zn:

Cd ratio such as that in the Indian Point sediments (100:1). This is due to the chemical similarity between Cd and Zn (same periodic family), and apparently they interact by competing for same uptake or binding sites. Thus, the already high Cd levels in the Indian Point plants could be suppressed by Zn at that site and under the proper conditions might become even greater.

The complexity and importance of geochemical processes in controlling bioavailability of cadmium and other metals in estuaries have been reviewed by Cross and Sunda (1978). Unlike most heavy metals, the bioavailability of cadmium increases when sediments become oxidized (Eh ca + 200 mv) and slightly acidic (pH 5 − 6). Gambrell *et al.* (1976) found that both rice (*Oryza*) and cordgrass (*Spartina*) accumulated the most Cd under these conditions. The seasonal pattern of Cd accumulation at the two extreme areas (Indian Point vs Redfish Bay) probably reflects the differences between the two areas in available Cd due to geochemical factors, as well as biological processes such as microbial activity and sediment reworking by infauna. These parameters ultimately affect the chemical speciation of cadmium, i.e., whether it is organically chelated, or complexed with inorganic ions (e.g. sulfide or chloride). The net effect of all these processes on bioavailability is impossible to predict. Therefore, it is important to know that bioaccumulation of a metal like Cd can be monitored on a yearly basis, using rooted seagrasses as indicator organisms.

High detrital and clay input to Upper Corpus Christi Bay probably acts to trap higher than normal levels of these metals, since clays and organic material are well-known for their metal-binding properties. Seagrasses growing on this type of sediment may even be stimulated to accumulate inordinate amounts of these metals. Levels of Zn in *Halodule* plants from Indian Point are three times higher (dry wt basis) than Zn in *Spartina alterniflora* growing on heavy metal-enriched sediments in a Massachusetts salt marsh studied by Banus *et al.* (1975). Cd found in *Halodule* during this study is as much as five times higher than in the same *Spartina*, despite the fact that the Indian Point sediments contain much less (only 10%) Cd than the Massachusetts salt marsh.

Since food may contribute more than 95% of the total body burden of some metals (Cross and Sunda 1978) to higher trophic levels, it is indeed significant that bioaccumulation of Cd and Zn can be documented for an important primary producer like *Halodule*. The fact that extensive beds of *Halodule* were growing in the Indian Point area suggests that these concentrations of heavy metals are not toxic to plant growth. This situation could lead to serious consequences through transfer of Cd to food chains. Heavy metals, including Cd, remain at high levels in seagrass and cordgrass detritus, rather than being leached out during decay (Banus *et al.* 1975, Pulich *et al.* 1976). Zooplankton (Bertram and Hart 1979; Marshall and Mellinger 1978) and shrimp (Nimmo and Bahner 1976), have been shown to be readily affected by Cd toxicity. These crustaceans (amphipods, isopods, shrimp, etc.) comprise the first link in the estuarine food chains which decompose seagrass detritus (Fenchel 1970, Harrison 1977) and would be the first organisms to graze on and consume Cd-rich seagrass detritus from this area.

ACKNOWLEDGMENTS

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SUMMER ASPECT OF ALGAL ZONATION ON A TEXAS JETTY IN RELATION TO WAVE EXPOSURE

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ABSTRACT

Forty-four species of benthic marine algae, including three species newly reported for the area, were collected in a quantitative study of species abundance and vertical ranges in relation to tide levels on exposed and sheltered vertical rocks at Port Aransas, Texas. Some species were selectively restricted to exposed or sheltered habitats, while species found in both environments typically presented a vertical displacement and obvious disparity in abundance between the two habitats. Characteristic communities of co-occurring species were found on both the sheltered and exposed sides. Similarity coefficients, expressed in composite trellis diagrams, demonstrated the relationship of algal zones to tidal levels and surf exposure.

INTRODUCTION

The general features of benthic marine algal zonation have been described for the warm temperate waters of the North Atlantic coast (Hoyt 1920, Williams 1949, Stephenson and Stephenson 1952, Earle and Humm 1964, Wulff and Webb 1969) and the Gulf of Mexico (Hedgpeth 1953, Edwards and Kapraun 1973, Kapraun 1974). With two exceptions (Earle and Humm 1964, Wulff and Webb 1969), these accounts were descriptive and provided no quantitative data for algal abundance or the vertical ranges of species in relation to accurately determined tide levels. Similarly, the effects of wave exposure on littoral algal zonation have been investigated in cool temperate (Burrows *et al.* 1954, Kingsbury 1962) and tropical regions (Stephenson and Stephenson 1950, Lawson 1966, van den Hoek 1969), but are relatively unknown in warm temperate waters. Consequently, this study of zonation on vertical rocks on the jetty at Port Aransas, Texas, was initiated to complement a previous ecological survey of the area (Edwards and Kapraun 1973) by providing binary data for vertical ranges and relative abundance for the summer jetty flora.

MATERIALS AND METHODS

Observations were made weekly between June 15 and July 15, 1978 on the southwest jetty at Port Aransas, Texas. The location and physical environment of this area have been previously

described (Edwards and Kapraun 1973). Vertical range and relative abundance of algal species were determined with a 1 M long belt quadrat divided into 10 × 10 cm^2 squares (Saito *et al.* 1976). Fourteen transects were made on individual vertical rocks, seven each on the channel (north side) and exposed (south side) of the jetty. All material was removed from each quadrat and identified in the laboratory. The inclusion of minute and epiphytic species prohibited a quantitative determination of abundance and percent cover (Saito and Atobe 1970). However, binary data for species present in each quadrat was used to estimate abundance and vertical range for each species.

The intersection of quadrats 5 and 6 was placed at mean low water (MLW) which was calculated from predicted low water (U.S. Dept. Comm. 1978) and a tide staff attached to a pier in the channel at the study site. Since the mean diurnal tidal range during the study was 47 cm with predicted maximum high and low water levels of + 52 and — 18 cm, respectively, the approximate mean high water level was at the intersection of quadrats 1 and 2.

The relationship of the algal composition among the 10 cm^2 quadrats was determined using Jaccard's coefficient (Wulff and Webb 1969) and illustrated in trellis diagrams (Hruby 1975, Russell 1972).

RESULTS

Forty-four species of benthic marine algae were collected in this study, including three species newly reported for the area: *Callithamnion cordatum*, *Cladophora prolifera*, and *Polysiphonia macrocarpa*. The vertical distribution and relative abundance for all species are summarized in Fig. 1. Ten species were found only on the channel side while eight species were collected only on the exposed south side. Several species which occurred on both sides of the jetty had conspicuously greater abundance on one side than the other, e.g. *Polysiphonia denudata*, *Rhodymenia pseudopalmata*, and *Dictyota dichotoma*. The abundance and vertical ranges of these species are schematically represented in Fig. 2.

Although some species were found throughout the vertical transects, characteristic communities of co-occurring species were observed on both the sheltered (Figs. 3–5) and exposed sides (Figs. 6–8). These communities are best described as consisting of a complex vertical gradient of overlapping species rather than as discrete zones marked by upper range limits of dominant species (Hughes and Thomas 1971).

In general, the channel side supports three well developed species groups: one centered around MHW (Fig. 3), one centered around MLW (Fig. 4), and the third in the subtidal (Fig. 5). Similarity coefficients for the channel transects reflect these groupings. The highest correlation (83%) between quadrats 5 and 6 results from an overlapping and superimposing of the lower and upper limits of upper littoral and subtidal species, respectively, in the region of MLW (Fig. 9).

The exposed side supports a greatly expanded mid littoral zone (Fig. 7) which includes a few upper littoral and subtidal species with extended vertical ranges, e.g. *Bryocladia cuspidata* and *Padina vickersiae*. Both the relative abundance and diversity of species characteristic of the upper littoral (Fig. 6) and subtidal zones (Fig. 8) are reduced on the exposed side. Similarity coefficients for the algal species in the exposed transects show two regions of high correlations, corresponding to a subtidal component, well defined but with reduced species diversity, and a mid littoral component, augmented by the upward deflection of some sublittoral fringe species (Fig. 10).

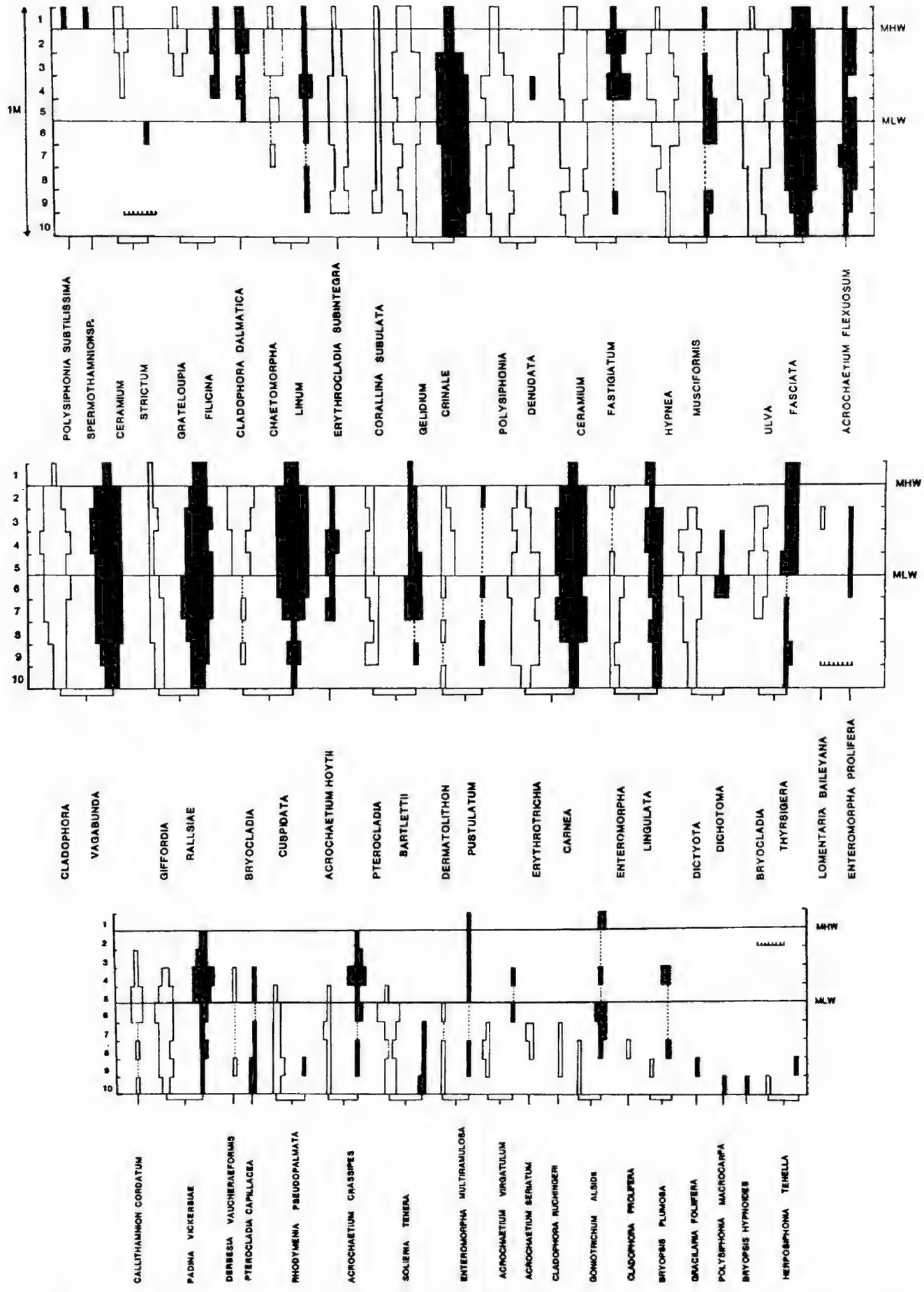

FIG. 1. Vertical ranges of species. Open columns = sheltered channel side. Closed columns = exposed south side. Scale = number of transects (1–7) in which species were collected for each quadrat level.

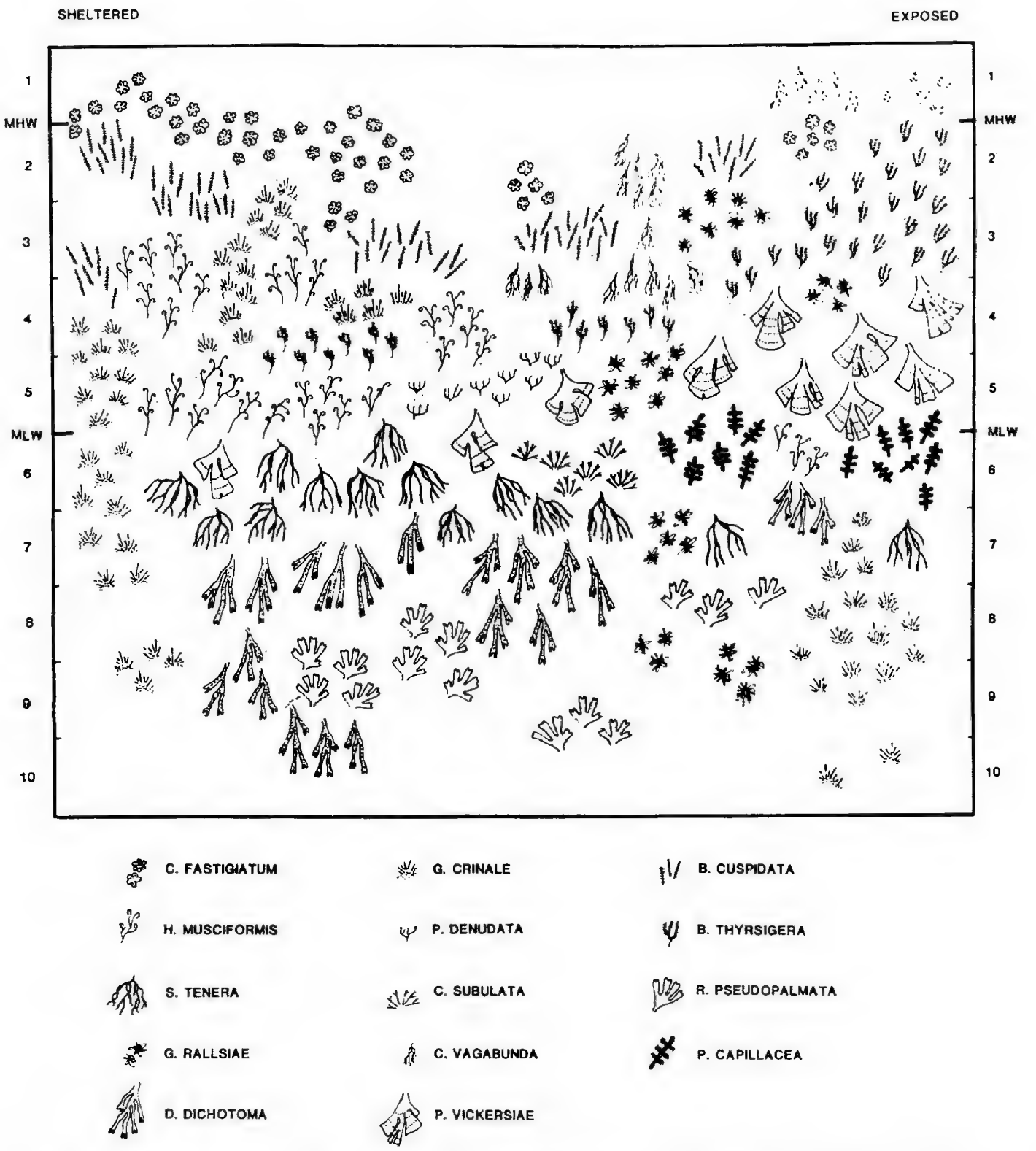

FIG. 2. Diagrammatic representation of vertical ranges and relative abundance of common species from sheltered and exposed habitats.

When the results of individual transects are collated to give a total number of species collected in particular quadrat levels for the channel and exposed rocks, the extent of upward deflection becomes apparent (Fig. 11). The maximum number of species on the channel side occurs in quadrat 8, while the maximum number on the exposed side occurs in quadrat 4.

DISCUSSION

The general features of the seasonal alternation of species and the fluctuations of their vertical ranges have been given elsewhere (Edwards and Kapraun 1973).

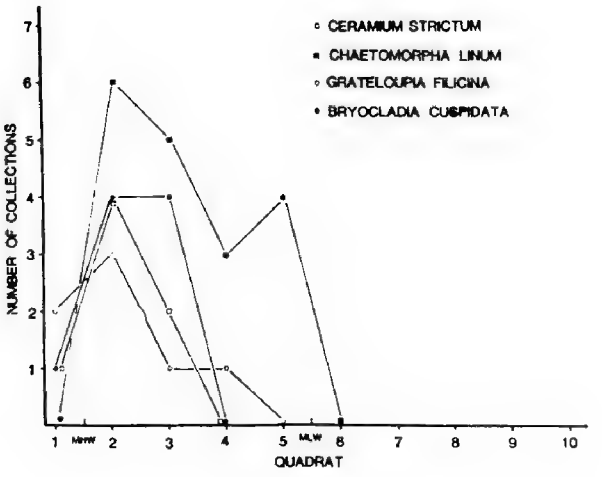

FIG. 3. Upper littoral.

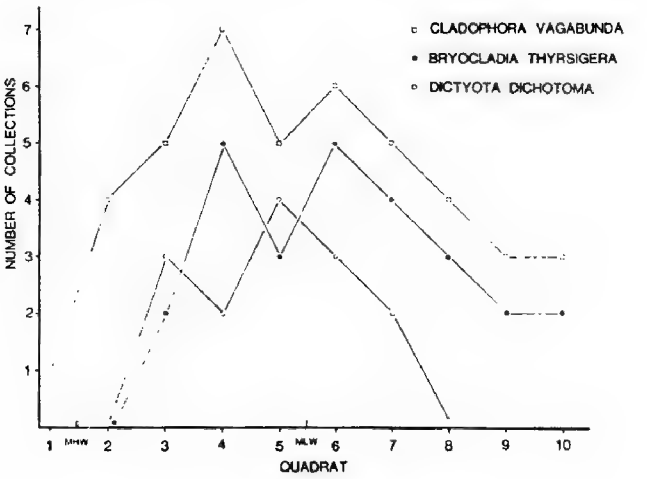

FIG. 4. Mid littoral.

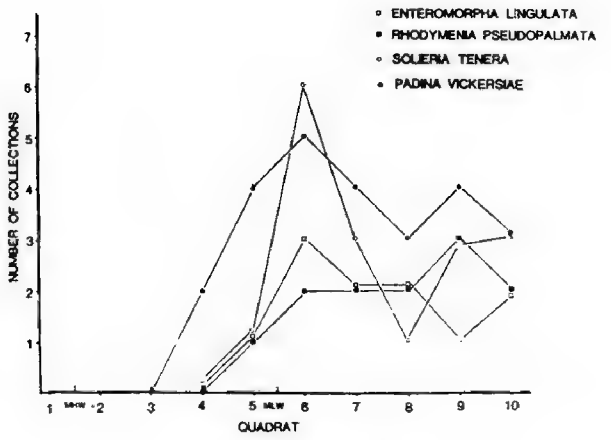

FIG. 5. Subtidal.

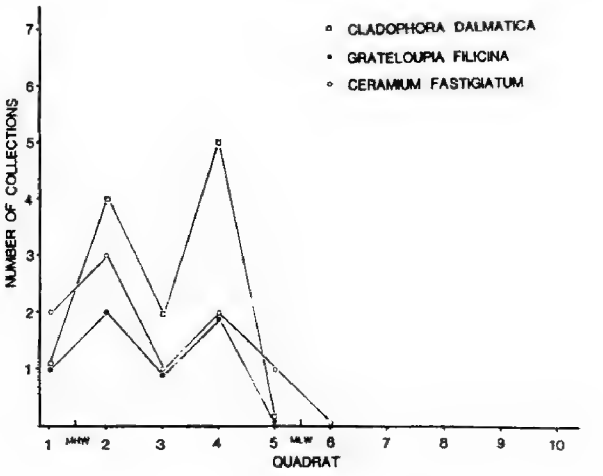

FIG. 6. Upper littoral.

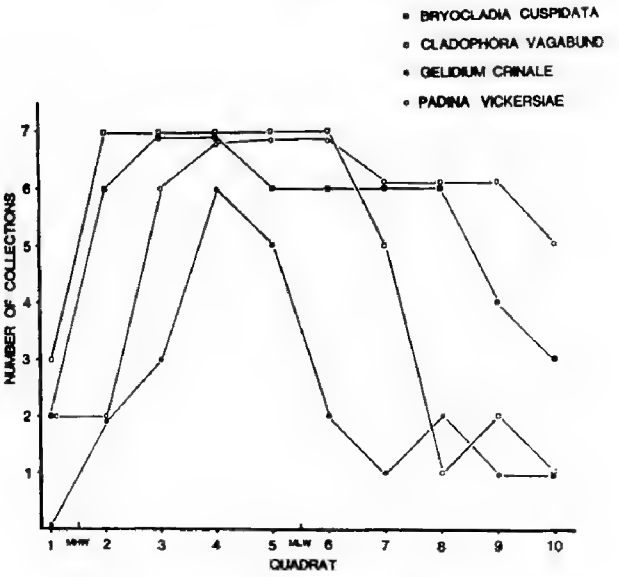

FIG. 7. Mid littoral.

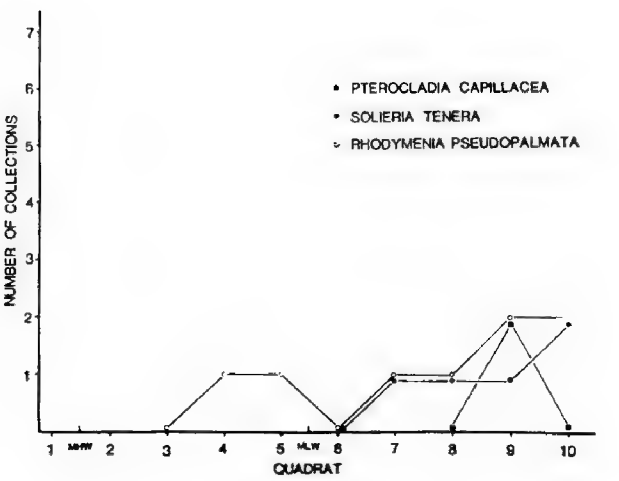

FIG. 8. Subtidal.

FIGS. 3–5. Relative abundance of dominant and indicator species in three benthic communities on the sheltered channel side.

FIGS. 6–8. Relative abundance of dominant and indicator species in three benthic communities on the exposed south side.

In the present study, 18 species were found to have distributions limited to either the channel or south side of the jetty. Although some of these taxa were subsequently found in general collections in both environments, the generalization still applies that species are differentially tolerant of exposure to surf (Kingsbury

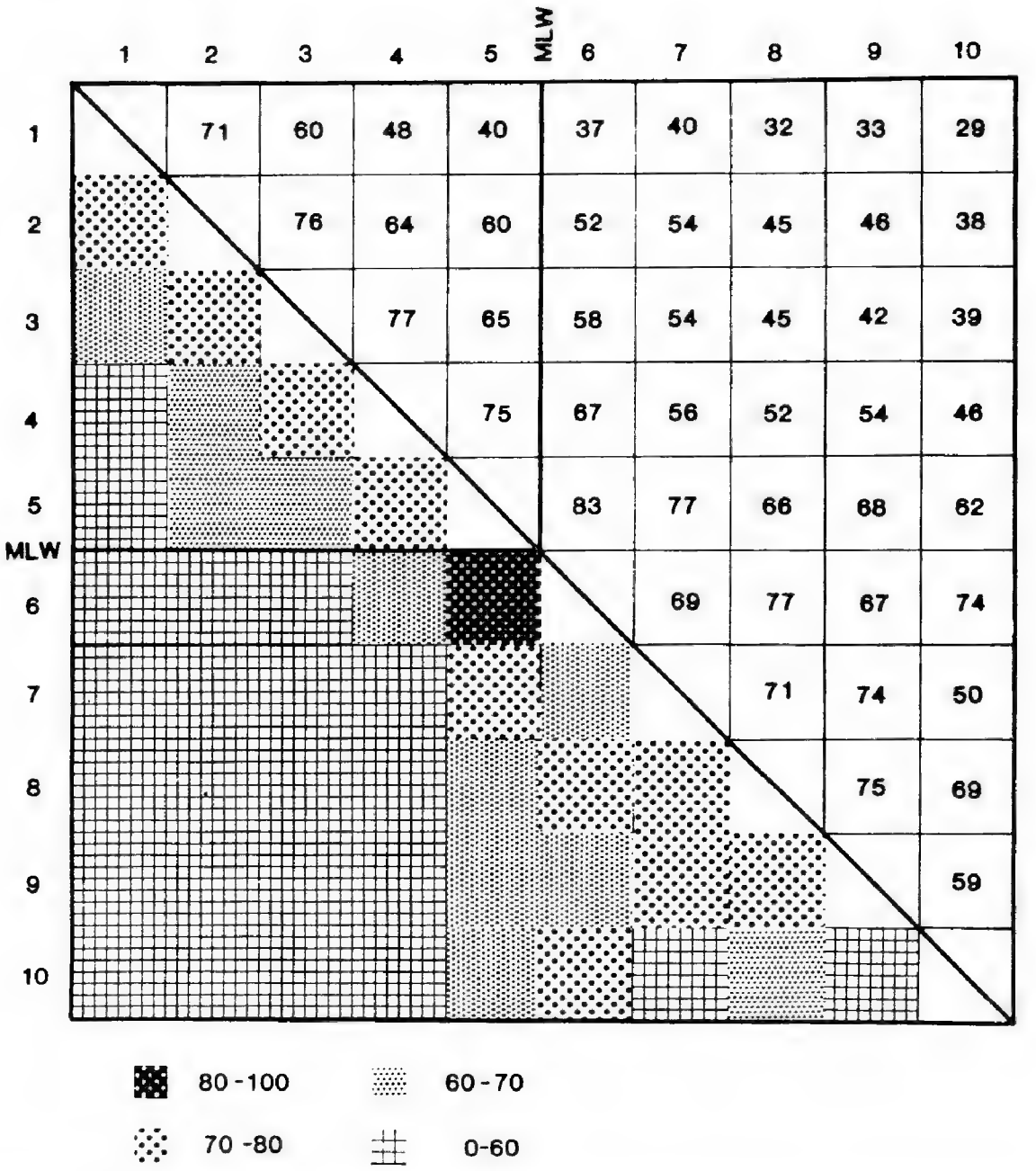

FIG. 9. Trellis diagram of similarity coefficients for sheltered channel transects.

1962, Lewis 1964, Widdowson 1964). *Corallina subulata*, *Polysiphonia denudata*, and *Callithamnion cordatum* were essentially restricted to the channel side where they achieved maximum abundance near mean low water, while *Cladophora dalmatica*, *Pterocladia capillacea*, and *Gracilaria foliifera* were most abundant on the exposed side. Restrictions imposed by a benthic alga's morphology on its distribution have been discussed (Doty 1971, Neushul 1972) and seem to apply to present observations. For example, species limited to protected sites are often delicately filamentous or articulated corallines, while species most abundant in surf-swept habitats are typically coarsely filamentous or cartilaginous with strap-shaped fronds.

Seven species of macroscopic algae had greater abundance or a conspicuous upward deflection of vertical ranges with increasing exposure. With the exception of *Bryopsis plumosa* and *Padina vickersiae*, these species were littoral, achieving maximum abundance between MLW and MHW. Perhaps the most interesting zonation pattern observed concerned the downward deflection of *Rhodymenia*

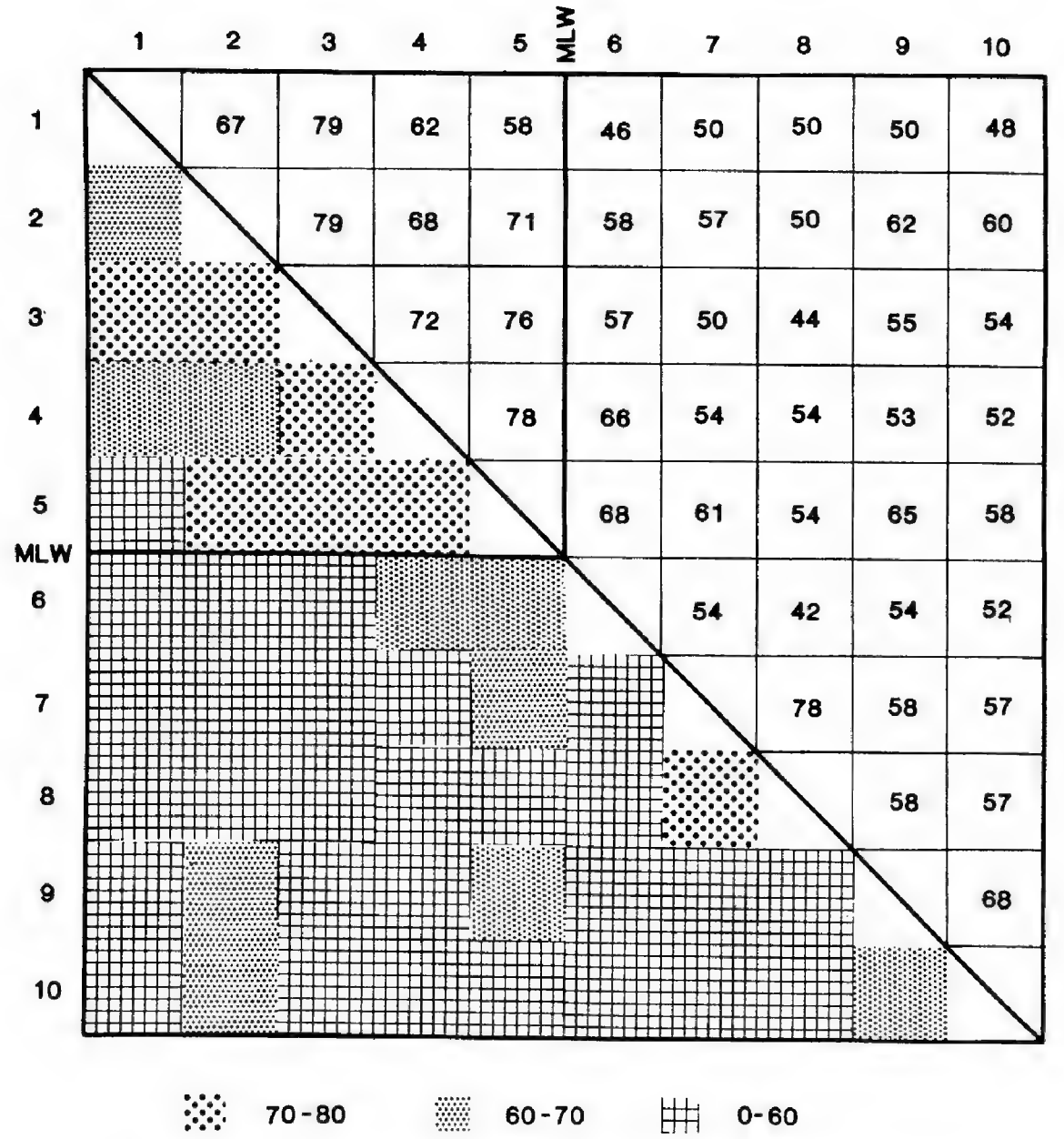

FIG. 10. Trellis diagram of similarity coefficients for exposed transects.

pseudopalmata and *Solieria tenera* with increasing exposure. It can be theorized that the fronds of these two species are susceptible to destruction by surge action. In British Columbia, Druehl (1967) found delicate algae removed by the physical action of waves, and thus occupying lower vertical zones in exposed habitats.

Lewis (1964) remarked that the upper littoral and upper subtidal algal zones are most similar between sheltered and exposed shores, while the greatest differences appear in the zone-forming species of the littoral. In this study, characteristic species of the upper littoral (Fig. 3) and subtidal zones (Fig. 5) were significantly less abundant on the exposed side (Figs. 6, 8), while there was a greater uniformity of species composition and abundance in the mid littoral (Figs. 4, 7). Further studies would be necessary to determine if these observations reflect the peculiarities of a particular environment, or if they have more general applicability to zonation in warm seas.

It is well known that wave action raises and broadens the bands of zonation for littoral algae (Burrows *et al.* 1954, Lewis 1964, Druehl 1967, den Hartog 1968, Åsen 1976). In this study, results of individual transects and similarity coefficients

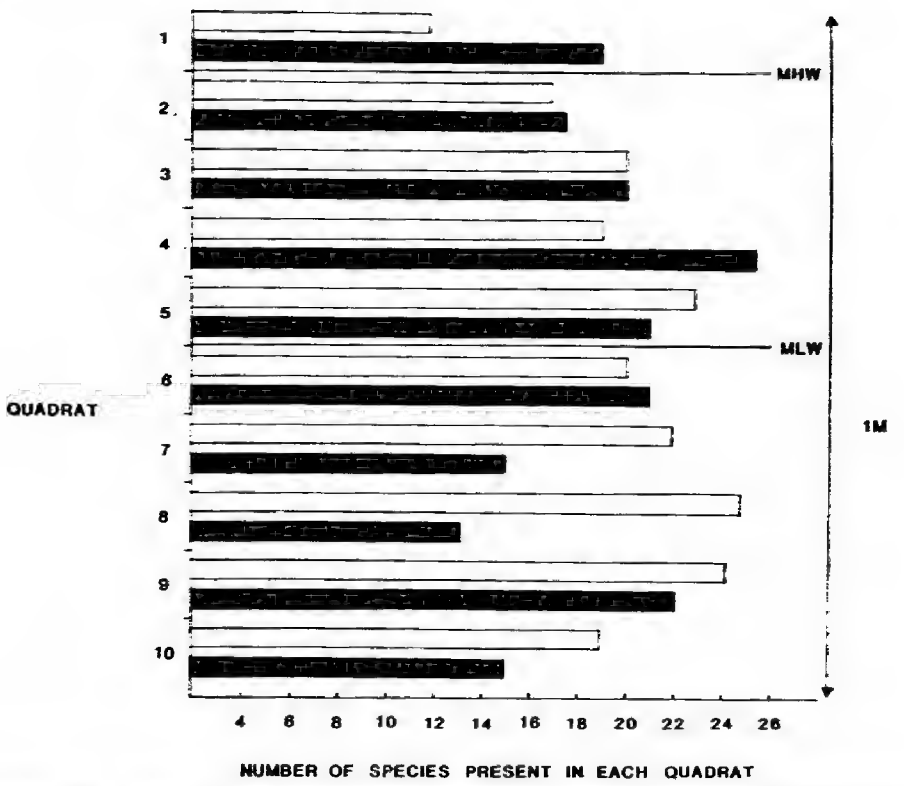

FIG. 11. Number of species in particular quadrat levels. Closed columns = exposed. Open columns = sheltered.

demonstrated a general upward deflection of subtidal species into the littoral, but the supralittoral remained essentially barren. The paucity of macroscopic algae above MHW, the narrowness of the mid littoral, and the weak development of the infralittoral fringe, as noted above, have been reported for tropical regions which have in common with the Texas coast a reduced tidal amplitude and elevated summer temperatures (Stephenson and Stephenson 1950, Lawson 1966, Rishardson 1969, van den Hoek 1969).

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THERMOREGULATORY BEHAVIOR OF A TROPICAL MARINE FISH: *FORCIPIGER LONGIROSTRIS* (BROUSSONET)

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Key Words: Thermoregulation, Behavior, Temperature preference, *Forcipiger longirostris*, Chaetodontidae, Marine, Tropical

ABSTRACT

Ten longnose butterflyfish, *Forcipiger longirostris* (Broussonet), were tested individually for 3-day periods in an Ichthyotron electronic shuttlebox to determine their ability to thermoregulate behaviorally. The range of voluntarily occupied temperatures for all individuals was 24–29°C. The mean thermal preferendum was higher at night (27.1°C) than during the day (25.3°C). The 24-hour mean final thermal preferendum was 26.3°C.

INTRODUCTION

The longnose butterflyfish *Forcipiger longirostris* (Broussonet) is relatively numerous on coral reefs at Kona, Hawaii (Hobson 1974). Like its congener, *F. flavissimus*, it is a diurnal predator that feeds throughout the day but remains inactive but alert close among coral or rock crevices at night (Hobson 1974). The two species overlap extensively at Kona, but where one is numerous, the other occurs less frequently; however, Hobson (1974) was unable to relate observed differences in relative numbers to specific habitat differences. The two species do differ somewhat in feeding habits, as *F. flavissimus* tears pieces off larger benthic animals, while *F. longirostris* does not (Hobson 1974).

While many fish species have been tested for ability to thermoregulate behaviorally (Richards, *et al.* 1977; Reynolds and Casterlin 1979, 1980a), most of the species tested have been temperate freshwater species. There has been a relative paucity of thermal preference and avoidance data for tropical marine fishes. Wallace (1977) reported experimental data on thermal preference of juvenile yellowtail snapper (Lutjanidae), *Ocyrus chrysurus*. Casterlin and Reynolds (1980) examined thermoregulatory behavior of *Canthigaster jactator* (Canthigasteridae), while Reynolds and Casterlin (1980b) studied thermal behavior of the surgeonfish (Acanthuridae) *Zebrasoma flavescens*. Medvick and Miller (1979) reported thermal preference behavior of several Hawaiian species, including the butterflyfish (Chaetodontidae) *Chaetodon multicinctus*. Apparently no other chaetodonts have been studied with respect to thermal behavior, so we

undertook a study of thermoregulatory ability of the longnose butterflyfish *Forcipiger longirostris*, the results of which are reported herein.

METHODS

Ten *Forcipiger longirostris* (102–118 mm TL) were purchased from a local aquarium dealer, who had recently received them by air freight from a supplier in Hawaii. The fish had reportedly not been treated with any chemicals. They were held at 20–22°C for 2–3 weeks in the laboratory prior to testing and fed dried brine shrimp prior to but not during testing, according to the standard procedures recommended by Richards, *et al.* (1977). The fish were tested individually for 3-day periods in Ichthyotron electronic shuttleboxes (described by Reynolds 1977) to determine their final preferenda (cf. Reynolds and Casterlin 1979, 1980a) by the "gravitation method." The tests were conducted with a natural photoperiod (May) provided through windows. Salinity (artificial sea salts) was 35 ‰. Data for all ten individuals were pooled, and analyzed to determine the thermoregulatory parameters (Table 1).

RESULTS

The fish voluntarily occupied a 24–29°C range of temperatures, with a 24-hour mean final preferendum of 26.3°C (Table 1). The preferendum was higher at night (27.1°C) than during the day (25.3°C). Thermoregulatory precision, measured by three different measures of dispersion, was greater by day than at night (Table 1).

DISCUSSION

The 24–29°C (Table 1) range of temperatures voluntarily occupied by *F. longirostris* in our tests is comparable to the 24.2–29.5°C range reported by Medvick and Miller (1979) for comparably tested *Chaetodon multicinctus*, another Hawaiian butterflyfish. *C. multicinctus* also reportedly exhibits diel differences in thermal preference, but in contrast to *F. longirostris*, it prefers higher temperatures during the day than at night (Medvick and Miller 1979). The reasons for this are unclear, since both species are diurnally active and have similar habitats (Hobson 1974).

Tropical reef species studied to date (Wallace 1977, Medvick and Miller 1979, Casterlin and Reynolds 1980, Reynolds and Casterlin 1980b, and Table 1) all

TABLE 1

Thermoregulatory parameters of *Forcipiger longirostris* (N = 10) tested individually in electronic shuttleboxes for 3 days each.

Parameter	Day	Night	24 hr
Mean (°C)	25.3	27.1	26.3
Mode (°C)	26	28	26
Median (°C)	25	27	26
Range (°C)	24–26	24–29	24–29
Midpoint (°C)	25	26.5	26.5
Standard Error (°C)	0.1	0.2	0.2
Standard Deviation (°C)	0.8	1.3	1.4
Skewness: (mean–mode)/S.D.	−0.9	−0.7	+0.2

apparently prefer temperatures between 20–30°C, which corresponds to the viable temperature range (19–30°C) for the reef-building corals with which they are associated (Jokiel and Coles 1977). The thermoregulatory behavior of these tropical marine reef species appears generally similar to that of warm temperate freshwater fishes (Richards, *et al.* 1977; Reynolds and Casterlin 1979, 1980a, 1980b; Magnuson, *et al.* 1979; Casterlin and Reynolds 1980), except that some of the latter species prefer temperatures exceeding 30°C (Reynolds and Casterlin 1976), as do some warm temperate marine fishes (Reynolds and Thomson 1974).

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TAGGING STUDIES OF RED SNAPPER (*LUTJANUS CAMPECHANUS*) AND VERMILION SNAPPER (*RHOMBOPLITES AURORUBENS*) OFF THE SOUTH TEXAS COAST[1]

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ABSTRACT

Two hundred ninety-nine red snapper (*Lutjanus campechanus*) and 793 vermilion snapper (*Rhomboplites aurorubens*) were tagged at six locations off the south Texas coast from May 1977 to January 1978. Fifty-six (5%) of the tags were returned (17 red and 39 vermilion snappers). The red snapper were free between 59 and 253 days, and the vermilion snapper were free between 30 and 847 days. Only three tag returns showed snapper movement, which was to adjacent banks or structures.

INTRODUCTION

The objective of this study was to determine the extent of the movements of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) off south Texas by tagging.

Snappers in the southeast United States are important to commercial and recreational fishermen. Recreational fishermen landed an estimated 17.3 million pounds (7,862.4 metric tons) of red snapper in 1970, and commercial fishermen landed 6.4 million pounds (2,903 metric tons) in 1977 (U.S. Dept. Commerce 1978).

The red snapper fishery off Texas developed in the 1880s, and by the turn of the century, the ports of Freeport and Brownsville were being supplied by small vessels with snapper that were caught on grounds already abandoned by large vessels (Camber 1955). The principal fishing grounds were off Galveston, but the banks off south Texas were also frequented.

Despite studies of the history of the Gulf snapper fishery (Jarvis 1935, Camber 1955, Carpenter 1965) and of the biology of the red snapper in Texas waters (Moseley 1966, Bradley and Bryan 1974), nothing is known about the movements of red or vermilion snapper off Texas.

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METHODS

Tagging took place at the following areas: Citgo Rig A-76, Baker Bank, Aransas Bank, Hospital Bank, Southern Bank and Dream Bank (Fig. 1). Longitude and latitude, depth, and number of tagged fish released for these areas are listed in Table 1. Fishes were tagged: in the spring (May 26–June 3, 1977) at Aransas, Hospital and Southern Banks; in the summer (July 24–28) at Citgo Rig A-76 and Baker Bank; in the fall (October 21–25) at Dream Bank; and in the winter (January 24–28) at Southern Bank.

Fish for tagging were caught on hook and line. Three fishing rods, each with 12-volt electric reels, were used at each tagging location. The terminal tackle consisted of five circle hooks on a 130-lb test monafilament leader and 1–2 lb (454–908 g) lead sinker. Frozen squid and fresh fish were used as bait.

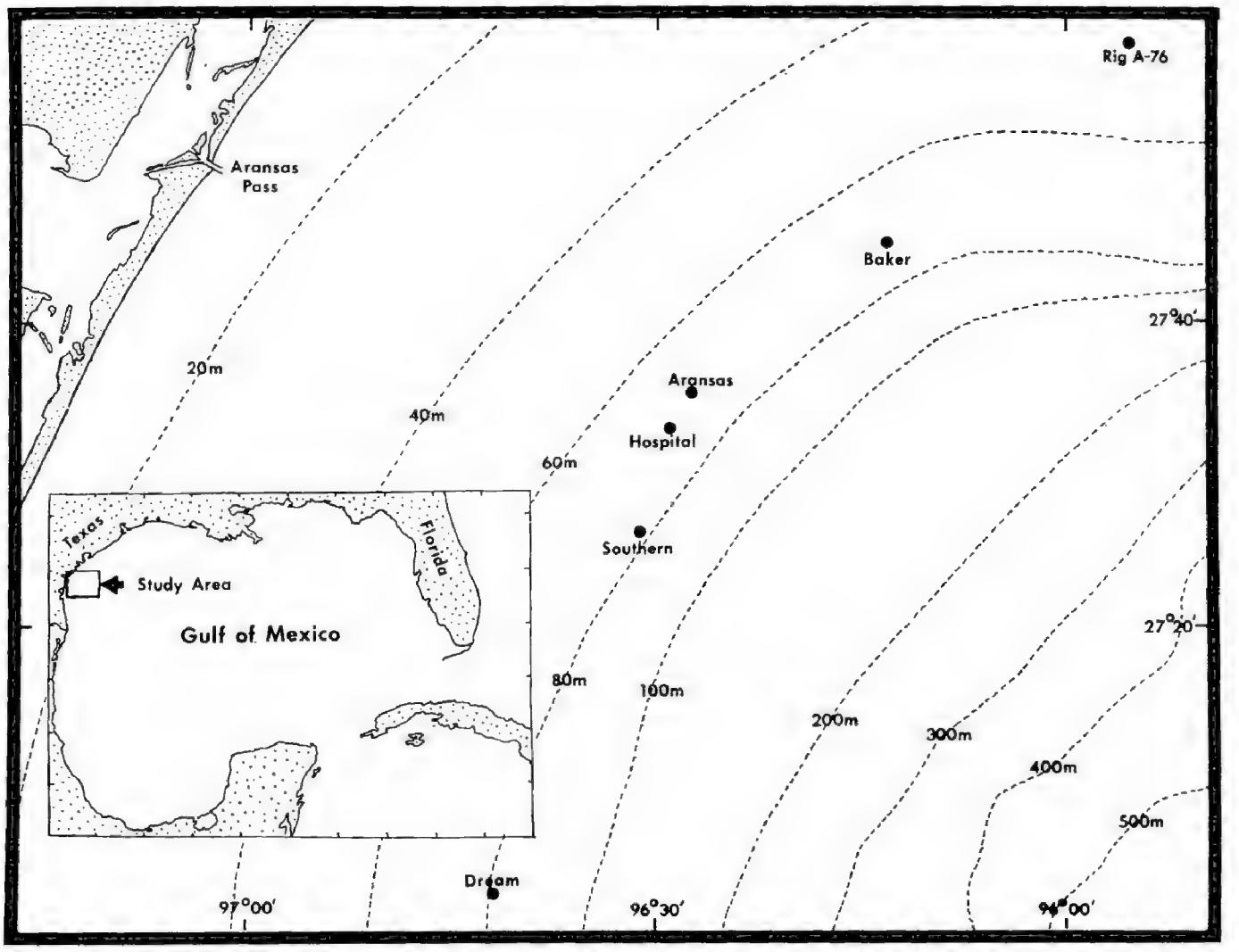

FIG. 1. Locations where snappers were tagged.

TABLE 1

Snapper tagging locations.

Name	Latitude x Longitude	Fishing Depths in Meters	No. tags released RS	VS
Citgo Rig A-76	27°58'N x 96°07'W	50	33	35
Baker Bank	27°45'N x 96°14'W	57	57	179
Aransas Bank	27°36'N x 96°27'W	60	148	314
Hospital Bank	27°33'N x 96°29'W	60	6	91
Southern Bank	27°26'N x 96°32'W	60	3	137
Dream Bank	27°02'N x 96°43'W	68	52	37

Most red snapper captured had expanded gases trapped in the body cavities. To allow fish to return to depths, we released the gases by puncturing the abdomens with a hypodermic needle.

All fishes to be tagged were measured to the nearest millimeter of fork length. They were tagged with a Floy gun tag at the base of the dorsal fin, and released at the surface. Tags were red, 3 inches (23.1 cm) long and had a legend: "Reward, NMFS, P.O. Box 1208, Port Aransas, TX." A tag number followed the legend.

Rewards between $5 and $25 were offered. Two preselected tag numbers out of each 100 were worth $25, five others were worth $10, and all others (93 out of 100) each were worth $5. Posters advertising the tagging study were placed at various locations around Port Aransas.

RESULTS AND DISCUSSION

Two hundred ninety-nine red and 793 vermilion snappers were tagged. Length-frequency distributions are shown in Figures 2 and 3. Size modes were 250–275 mm FL for red snapper and 225–250 mm FL for vermilion snapper.

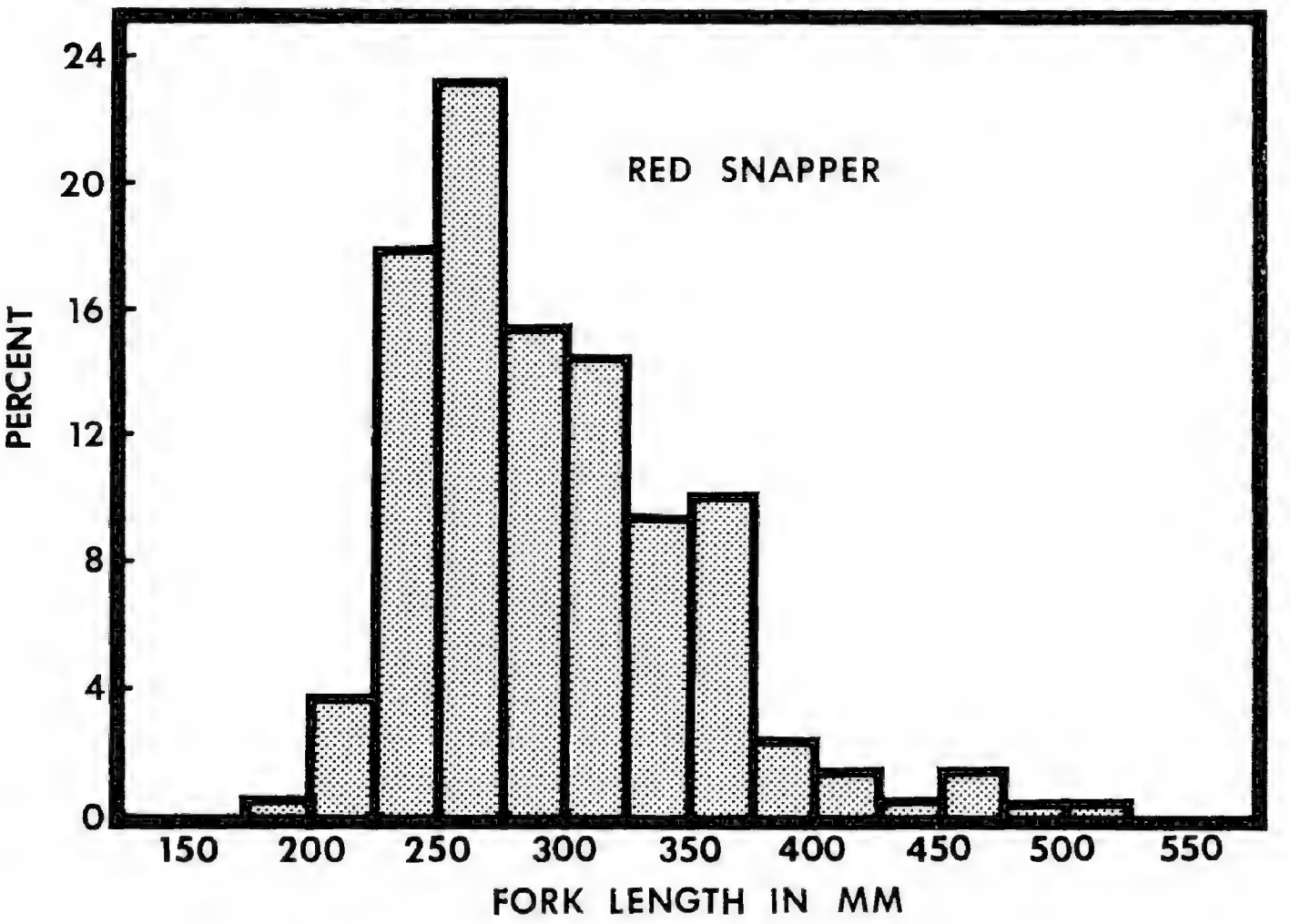

FIG. 2. Length-frequency distribution of 299 tagged red snapper.

Return Rates

The return rate for red snapper was 5.6% (17 tags) and for vermilion snapper was 4.9% (39 tags). Table 2 shows that other researchers had higher red snapper return rates (12.5–33.0%) but lower vermilion snapper return rates (0–4.1%). Generally, sizes of snappers tagged by the other researchers were similar to the sizes we tagged. Differences between return rates among these investigators may be attributable to differences in fishing pressure. Red snapper were heavily fished

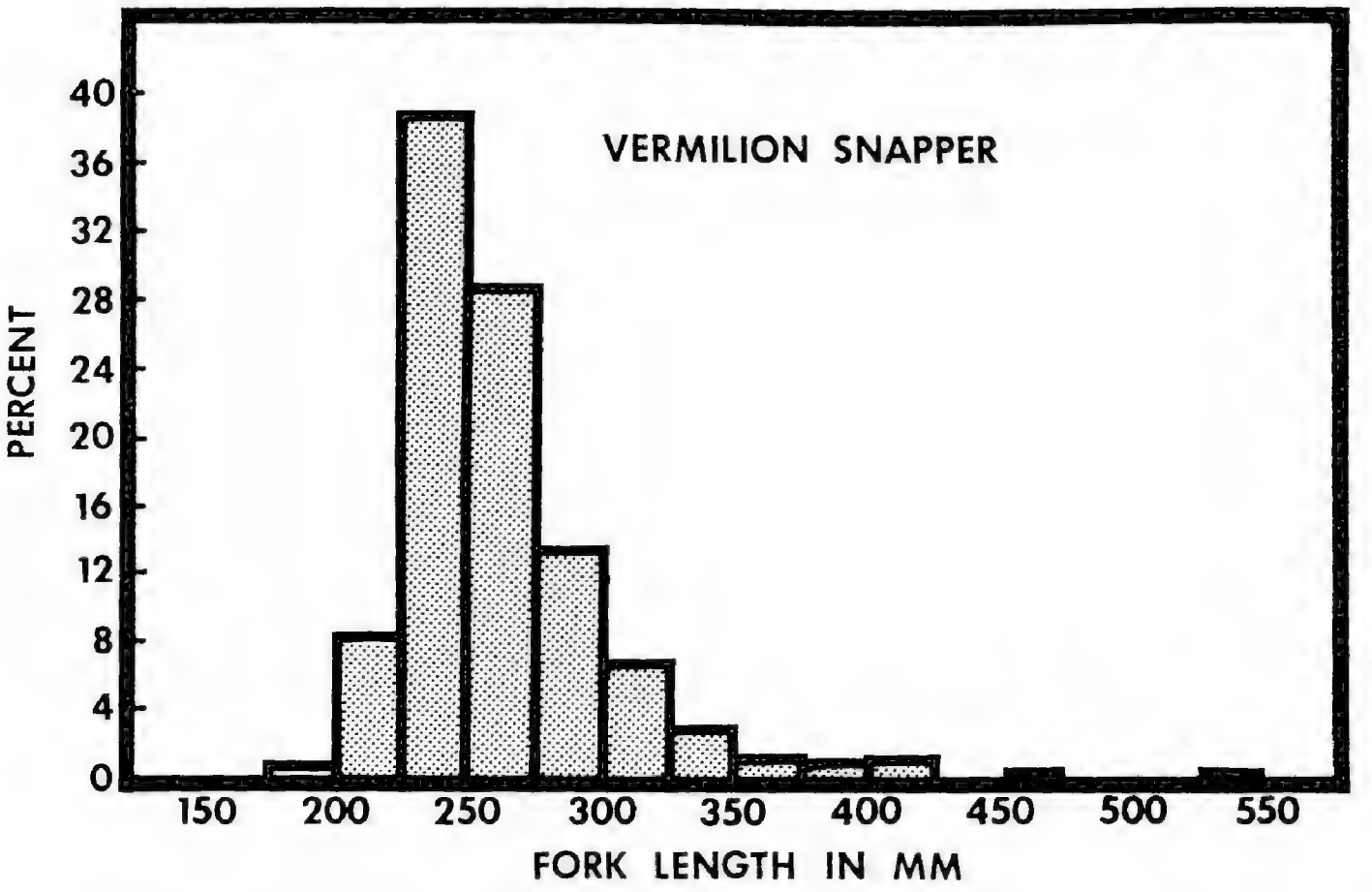

FIG. 3. Length-frequency distribution of 793 tagged vermilion snapper.

TABLE 2

Summary of other snapper tagging studies.

Author(s)	No. Tagged	No. Returned	Return Rate
	Red Snapper		
Topp, 1963	379	65	17.2%
Beaumariage, 1964	336	111	33.0%
Beaumariage and Wittich, 1966	345	97	28.1%
Moe, 1966	24	3	12.5%
Beaumariage, 1969	312	82	26.3%
Beaumariage, 1969 (includes all above authors except Moe)	1,372	384	28.0%
	Vermilion Snapper		
Topp, 1963	117	0	0.0%
Beaumariage, 1964	218	9	4.1%
Beaumariage and Wittich, 1966	57	0	0.0%
Moe, 1966	13	0	0.0%
Beaumariage, 1969	4	0	0.0%
Grimes, 1976	455	2	0.4%

in Florida, where most of the other tagging occurred, but vermilion snapper were usually considered a nuisance (Moe 1963). In the Carolinas (Grimes 1976) and in Texas, both species are valued. In fact, the vermilion is the most frequently angled snapper in the Carolinas (Grimes *et al.* 1977).

Movement

There was very little movement by either species (Table 3). No movement was indicated by returns of any of the 48 tags at large less than 160 days. Of the eight at large longer, three showed movement to an adjacent bank or oil rig. Of these

TABLE 3

Data on snapper tag returns (V = vermilion snapper; R = red snapper).

Tag No.	Sp.	Tag Date	Return Date	Days Out	Tagging Location	Return Location	Km. Trav.	FL at Tagging (mm)	FL at Return (mm)	Length Change
15058	V	5-31-77	6-30-77	30	Southern	Same	0	255	255	0
15107	V	5-31-77	7-7-77	37	Southern	Same	0	230	240	+10
15215	V	6-2-77	7-9-77	37	Hospital	Same	0	290	290	0
10357	V	5-29-77	7-26-77	58	Aransas	Same	0	235	235	0
10964	V	5-28-77	7-26-77	59	Aransas	Same	0	290	290	0
10395	V	5-28-77	7-26-77	59	Aransas	Same	0	242	230	-12
10974	V	5-28-77	7-26-77	59	Aransas	Same	0	220	230	+10
15087	V	5-31-77	8-6-77	67	Southern	Same	0	250	250	0
10970	V	5-28-77	8-9-77	73	Aransas	Same	0	230	-	-
10151	V	5-30-77	8-23-77	85	Aransas	Same	0	240	240	0
10170	V	5-30-77	8-23-77	85	Aransas	Same	0	250	260	+10
10182	V	5-30-77	8-23-77	85	Aransas	Same	0	240	230	-10
09402	V	5-29-77	8-23-77	86	Aransas	Same	0	230	225	-5
10352	V	5-28-77	8-23-77	87	Aransas	Same	0	225	265	+40
10427	V	5-28-77	8-23-77	87	Aransas	Same	0	265	255	-10
10433	V	5-28-77	8-23-77	87	Aransas	Same	0	235	220	-15
10494	V	5-28-77	8-23-77	87	Aransas	Same	0	250	240	-10
10499	V	5-28-77	8-23-77	87	Aransas	Same	0	227	225	-2
09547	V	5-27-77	8-23-77	88	Aransas	Same	0	230	220	-10
09557	V	5-27-77	8-23-77	88	Aransas	Same	0	240	225	-15
10110	V	5-30-77	8-25-77	87	Aransas	Same	0	250	245	-5
10140	V	5-30-77	8-25-77	87	Aransas	Same	0	225	230	+5
09689	R	5-29-77	8-25-77	88	Aransas	Same	0	295	310	+15
10410	V	5-28-77	8-25-77	89	Aransas	Same	0	235	240	+5
10447	V	5-28-77	8-25-77	89	Aransas	Same	0	235	230	-5
10492	V	5-28-77	8-25-77	89	Aransas	Same	0	240	235	-5
09384	R	5-27-77	8-25-77	90	Aransas	Same	0	360	335	-25
09408	V	5-27-77	8-25-77	90	Aransas	Same	0	230	225	-5
09546	R	5-27-77	8-25-77	90	Aransas	Same	0	280	304	+24
09693	R	5-29-77	9-11-77	105	Aransas	Same	0	255	270	+15
09704	V	5-29-77	9-11-77	105	Aransas	Same	0	255	255	0
10448	R	5-28-77	9-11-77	106	Aransas	Same	0	240	245	+5
10114	V	5-30-77	9-15-77	108	Aransas	Same	0	255	250	-5
10094	V	5-30-77	9-15-77	108	Aransas	Same	0	245	241	-4
10375	V	5-29-77	9-15-77	109	Aransas	Same	0	235	265	+30
10381	V	5-29-77	9-15-77	109	Aransas	Same	0	265	251	-14
10487	R	5-28-77	9-15-77	110	Aransas	Same	0	255	260	+5
09393	R	5-27-77	9-15-77	111	Aransas	Same	0	230	267	+37
10979	V	5-28-77	9-20-77	115	Aransas	Same	0	260	257	-3
15283	R	7-24-77	9-21-77	59	Baker	Same	0	470	-	-
15298	R	7-24-77	9-21-77	59	Baker	Same	0	350	-	-
15308	R	7-24-77	9-25-77	63	Baker	Same	0	295	295	0
10134	V	5-30-77	10-4-77	127	Aransas	Same	0	225	225	0
10485	R	5-28-77	10-4-77	129	Aransas	Same	0	250	260	+10
09690	R	5-29-77	10-8-77	132	Aransas	Same	0	230	240	+10
10980	R	5-28-77	10-8-77	133	Aransas	Same	0	240	255	+15
09541	V	5-27-77	10-8-77	134	Aransas	Same	0	250	250	0
10141	V	5-30-77	10-25-77	151	Aransas	Same	0	265	250	-15
10367	V	5-29-77	11-15-77	170	Aransas	Hosp./South.	10-20	235	235	0
10442	V	5-28-77	11-15-77	171	Aransas	Hosp./South.	10-20	245	240	-5
09366	V	5-27-77	11-15-77	172	Aransas	Same	0	248	235	-13
09697	R	5-29-77	12-31-77	215	Aransas	Same	0	225	244	+19
15524	R	7-26-77	1-4-78	162	A-76	A-100	5	280	-	-
09558	R	5-27-77	1-7-78	224	Aransas	Same	0	240	264	+24
10989	R	5-27-77	2-4-78	253	Aransas	Same	0	250	230	-20
15554	V	7-26-77	11-20-79	847	A-76	Same	0	210	480	+270

three, two were vermilion snapper which, in 170 days moved from Aransas Bank to either Hospital (10 km) or Southern Bank (20 km)—the fisherman was unsure of the capture location. The third return was of a red snapper tagged at Citgo Rig A-76 and recaught at another rig about 5 km away after 162 days.

In summarizing the red snapper tagging in Florida, Beaumariage (1969) found that fish tagged in less than 27.4 m of water moved little, but ten returns suggested that fish released in deeper water moved more. These returns were from fish of a similar size to those we tagged. Seven of these ten returns showed easterly movement off northwest Florida. Eight of the ten were free for over 240 days. Only two of our 56 recaptured fish were at large this long.

Grimes *et al.* (1977) stated that vermilion snapper are apparently nonmigratory. Neither the two returns reported by him in 1976 nor the nine returns reported by Beaumariage (1964) showed any movement. Of the 39 returns from this study, only two showed even slight movements.

Length Change

There is a great variation in the change in length of returned snappers (Table 3) and many fish became shorter. Topp (1963) suggested that shrinkage caused by drying and freezing recaptured fish, and the adverse effects of tags on the activities of fishes preclude basing conclusions about growth on recaptured fish.

Predation

Predation of newly tagged fishes was observed in two instances. Once greater amberjack (*Seriola dumerili*), and once great barracuda (*Sphyraena barracuda*) were the predators. The amount of predation below the surface was unknown, but may have been considerable. Topp (1963) discussed this problem and concluded that it will always be a concern in deep-water tagging. Predation might have been minimized by using a cage in which snappers could have been lowered to the bottom and then released.

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THE OCCURRENCE OF SEA TURTLES ON THE SOUTH TEXAS COAST[1]

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ABSTRACT

The results of a three-year survey of sea turtles on south Texas beaches indicates that they are stranded most frequently in April–May and November and most often on Mustang Island and the northern half of Padre Island. The number of strandings has increased from 1976 to 1979. Loggerheads (*Caretta caretta*) are the most common sea turtle as indicated by the number of turtles washed ashore on beaches and by those seen around hard bottom features nearshore. The majority are subadults. Information on the strandings, occurrence and life history of four other species in south Texas coastal waters is detailed.

INTRODUCTION

At one time, turtles in excess of 500 lbs were commercially netted in the shallow bays near Port Aransas, Texas (Harwood and Scrivner 1949). These were probably green sea turtles (*Chelonia mydas*) which still enter south Texas bays. Although sea turtles are no longer abundant enough to be commercially exploited along the Texas coast, they are still common in the northwestern Gulf of Mexico. Loggerheads (*Caretta caretta*) are commonly seen in coastal waters and are frequently stranded on south Texas beaches. In 1977 and 1979, loggerheads nested on South Padre Island (H. H. Hildebrand, personal communication). The largest sea turtle nesting beach in the northwestern Gulf is that of Kemp's ridley (*Lepidochelys kempi*) at Rancho Nuevo, Mexico 300 km south of the Rio Grande River (Hildebrand 1963). Records of sporadic nesting by this (Werler 1951, Francis 1978) and other species have been documented for the Texas coast (Hildebrand 1963). A large concentration of approximately 100 leatherback turtles (*Dermochelys coriacea*) was reported off St. Joseph's and Matagorda Islands in December 1956 by Leary (1957). Leatherbacks, except for occasional feeding aggregations, and hawksbills (*Eretmochelys imbricata*) are rare along the Texas coast.

Because of the inherent difficulty of studying sea turtles in areas where they do not nest regularly, data concerning sea turtle populations along the Texas coast are limited. Most available information is derived from turtle stranding records and

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occasional *in situ* observations. Increased interest in endangered and threatened species interaction with fisheries and lack of quantifiable data on sea turtles prompted us to obtain and consolidate data for the south Texas coast.

METHODS

The study area encompassed 208 km of the south Texas barrier island chain from Cedar Bayou to Brazos Santiago Pass and included St. Joseph's, Mustang and Padre Islands (Fig. 1). The sandy foreshore of the barrier island beach is generally sloping with a landward ridge of vegetated dunes. The inner continental shelf seaward of the barrier island is predominantly a featureless silty sand bottom. Naturally occurring hard substrates on the nearshore (less than 30 m) shelf are rock outcroppings such as 9-Fathom Rock, 7½-Fathom Reef and Steamer Reef (Fig. 1). Man-made, artificial structures such as jetties, seawalls and oilfield production platforms are additional topographic features.

For three years (1976–1979) data on sea turtles were compiled from our examination of stranded turtle carcasses and sightings of live turtles in coastal waters, as well as from additional reports by agencies and individuals. Most observations were made by periodically driving the length of the barrier island beaches to look for turtles washed ashore. Personnel of Padre Island National Seashore, National Marine Fisheries Service Enforcement Division and Nueces County Parks Department worked closely with us to provide information on stranded turtles. Additional sightings were reported by interested citizens, who either recorded the data or reported sightings to us which we then examined. Persons examining carcasses and collecting data were instructed in turtle identification and provided with data forms to be completed. Information collected included species, location, sex (if determinable), straight line measurements of carapace and head length and width, notable deformities, fouling organisms and other identifying marks. Measurements in the text refer to straight line carapace length unless otherwise specified. To avoid duplication of effort by data gatherers, carcasses were disposed of behind the primary dune line.

RESULTS

Two hundred fifty-nine (259) sea turtles of 4 species were recorded in the study area from September 1976 through September 1979. Thirty-one (31) carcasses were not identified to species. Turtles were most frequent in April–May and November (Fig. 2) when 58% and 13%, respectively, of the total strandings for all 3 years occurred. The number of turtle strandings increased through the 3 years. In 1976, 21 turtles were observed in the last 4 months of the year. Observations increased to 26 for 1977, 100 for 1978 and 112 for the first 9 months of 1979. For the period September–August, numbers of turtles increased from 41 to 69 to 149 for each of the three years.

Sea turtles most frequently washed ashore on North Padre Island (30.5%) and the Little Shell and Big Shell beaches of Padre Island (29.0%) (Fig. 1). Lesser numbers occurred on Mustang Island beaches (18.2%), the area of Padre Island north of Mansfield Pass (8.9%), South Padre Island (7.3%), St. Joseph's Island (4.3%) and the Upper Laguna Madre, Corpus Christi Bay and Aransas Bay (1.9%).

The loggerhead was most often recorded (202 individuals). They were found during all months except January and February and were most abundant in April–May and November (Fig. 2). The average carapace length was 70 cm and ranged from 50.5 to 92.5 cm (Fig. 3). Most (98%) were smaller than the size re-

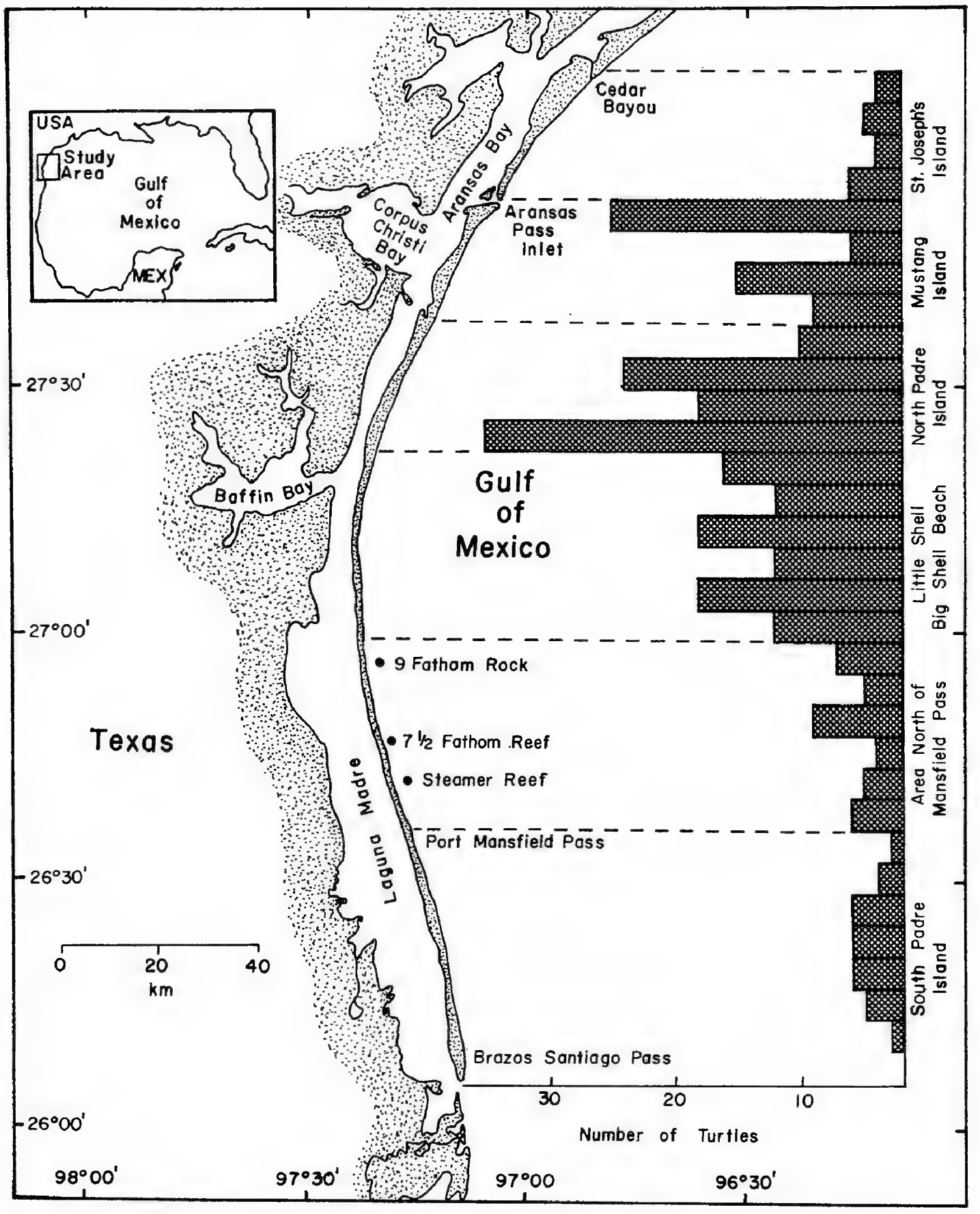

FIG. 1. Location of study area and number of stranded sea turtles recorded by distance along south Texas beaches (1976–1979).

ported by Hillestad, Richardson and Williamson (1978) for adult potentially breeding loggerheads (76 cm) stranded on Georgia beaches. Eight percent (8%) were larger than the smallest nesting loggerhead (81 cm) reported by Ehrhart and Yoder (1978) from Merritt Island, Florida. One male (82 cm) was reported in April 1979.

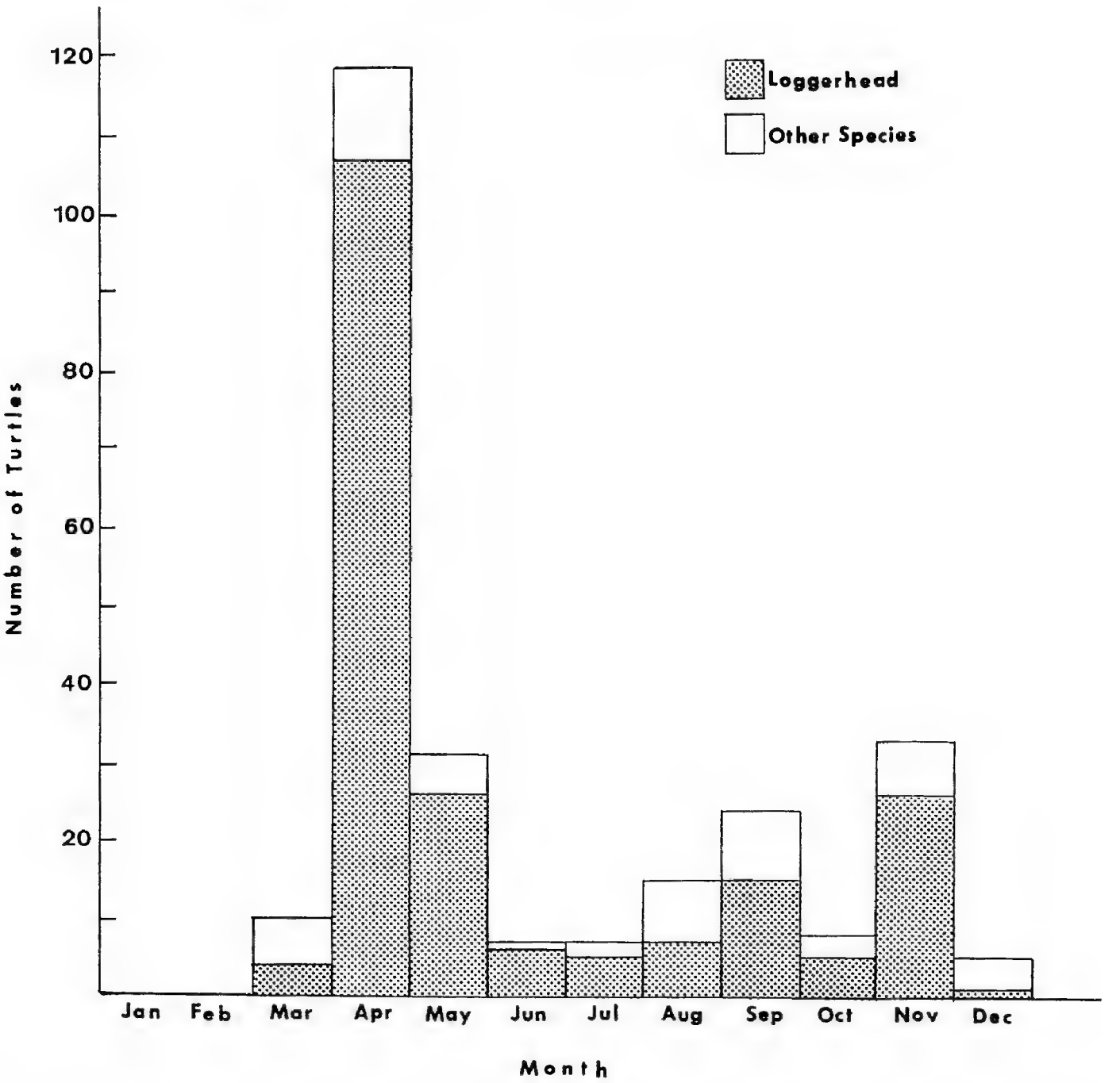

FIG. 2. Number of stranded sea turtles recorded by month for 3 years (1976–1979) on south Texas beaches.

The high frequency of stranded loggerheads was paralleled by the number of live individuals seen in shallow, offshore areas near hard substrates. Loggerheads were frequently seen near offshore oil platforms, natural rock reefs, and rock jetties in the study area. Stomach contents were not analyzed regularly during the study, but were sometimes examined inadvertently when an individual had decomposed to the point that the contents of the stomach spilled onto the ground. The presence of sea urchin spines in these stomach contents indicates feeding preferences which may account for loggerhead occurrences near hard bottom features. One autopsied specimen contained *Sargassum* seaweed, bird feathers and pieces of a plastic bottle in its digestive tract (B. Fuls, personal communication).

Fifteen Kemp's ridleys were counted, six of which were hatchlings or recent post-hatchlings (4.5 to 7.6 cm). Seven, according to the size categories of Carr (1952), were subadult (14.5 to 51.9 cm), and two were adults (62 and 66 cm).

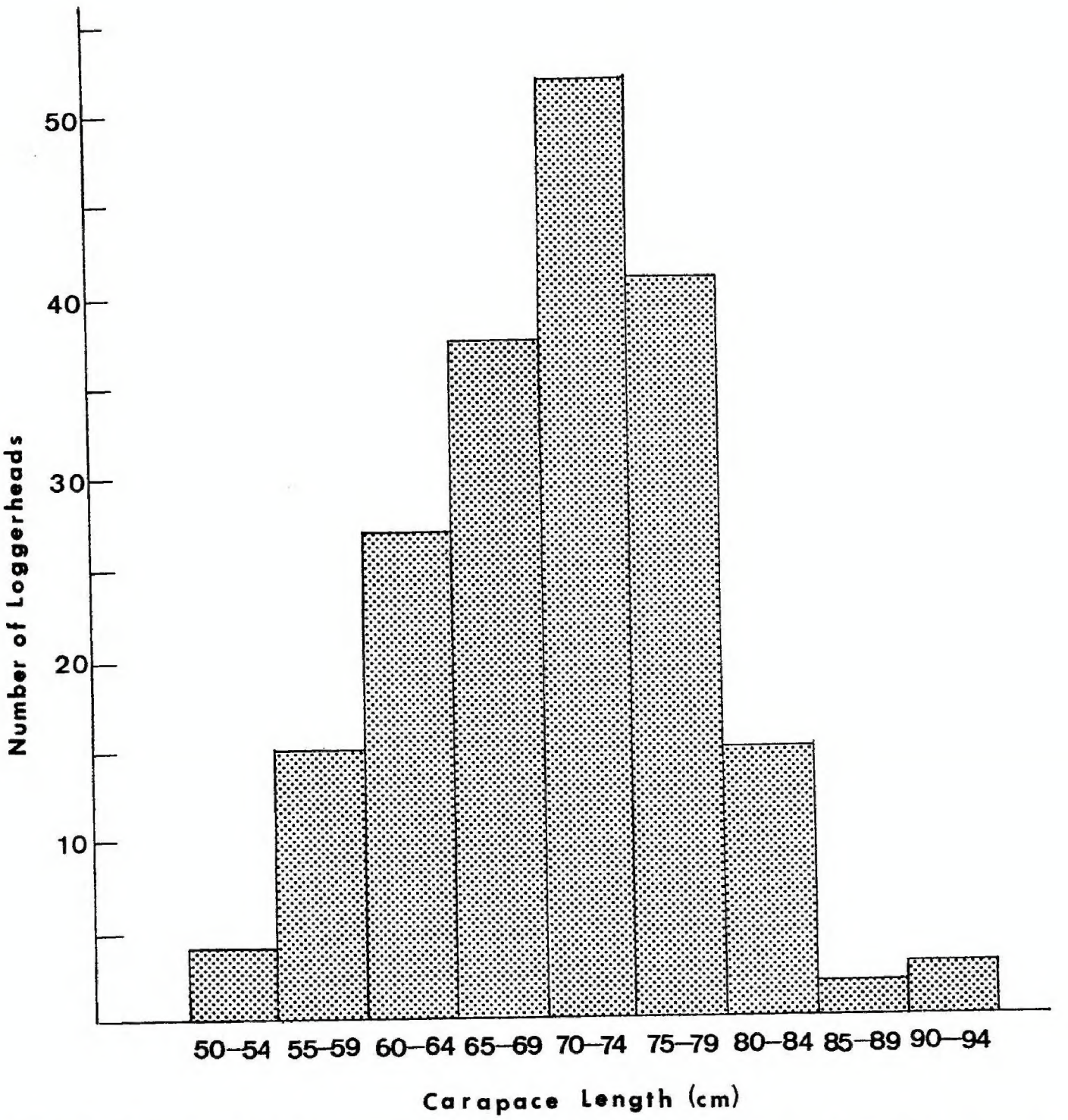

FIG. 3. Size (straight line carapace length) of loggerhead turtles washed ashore on south Texas beaches (1976–1979).

Francis (1978) reported hatchlings from ridley nests on South Padre Island in May 1974 and July and August 1976. One ridley nested on North Padre Island in June 1979 (R. G. Whistler, personal communication). During our 3-year survey, hatchlings washed ashore in August 1977 and July, August and early September of 1979. These strandings correspond with hatchling emergence at Rancho Nuevo in mid-June to mid-August. Subadults were found in April–May and September–October; and the adults, in October.

Ten green sea turtles were found. Three (29.8 to 34.0 cm) were reported from coastal bays. One (88.9 cm) was stranded on Mustang Island less than 1 km from Aransas Pass Inlet, and one hatchling (7.6 cm) washed in on North Padre Island. During 22–31 August 1979, five juvenile greens (20 to 21 cm) washed ashore on

Padre and Mustang Islands. All were heavily fouled with oil, which may have contributed to their deaths. The heaviest concentrations of oil from the Ixtoc I well blowout in the Bay of Campeche washed ashore on Mustang and Padre Islands on 23 and 24 August 1979 (Amos 1980).

One dead leatherback, approximately 150 cm, was observed floating off the Aransas Pass Inlet jetties in May 1977. No hawksbills were observed in the study but they do occur rarely in south Texas waters. Four hawksbills (less than 20 cm) were seen live off the Aransas Pass Inlet jetties in late summer from 1970 to 1975 (personal observations).

DISCUSSION

The increase in the number of sea turtles strandings through the 3-year study may be an artifact of increased sampling effort, but we and the people who helped collect the data feel that a real increase in strandings did occur in 1978 and 1979. No definite cause was established but an increase in trawling activity in nearshore waters during periods of the highest incidence of strandings may reinforce the view presented by Hillestad *et al.* (1978) that shrimp trawlers figure heavily in the premature death of many sea turtles. The greater frequency of turtle strandings along certain portions of the coast (Little Shell and Big Shell beaches of Padre, North Padre Island and Mustang Island) may substantiate this view since increased trawling activity in nearshore waters was documented in these areas when turtle strandings were occurring. Differences in sampling effort and the influence of longshore and nearshore currents, however, may also account for some of the locality-related differences in numbers of strandings.

Loggerheads, the majority of which were subadults, were the common sea turtles on the south Texas coast. Mature loggerheads may be rare in this portion of the Gulf of Mexico. Kemp's ridleys were the second most common species but their occurrence was infrequent. The occurrence of ridley hatchlings on area beaches was probably due to the close proximity of the nursery area at Rancho Nuevo, Mexico, the sporadic nesting of ridleys on Padre Island, and the recent efforts of Mexican and United States wildlife agencies to augment survival of this endangered species. The beach stranding data indicate that juvenile greens may spend a portion of their lives in the open northwestern Gulf of Mexico. Limited observations of hawksbills and leatherbacks indicate that they are rare along the south Texas coast.

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